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# The climatic challenge: Which plants will people use in the next century?

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**Highlights**

- >31,000 plants have documented uses, but humans fulfil most requirements with very few species.
- Future selection pressures on useful plants are likely to be different to those during domestication.
- Society faces two trade-offs; substitution vs adaptation and specialization vs diversification.

- Continued biodiversity loss, in part due to climate change, will further erode our choice of future strategies.

## Abstract

More than 31,000 useful plant species have been documented to fulfil needs and services for humans or the animals and environment we depend on. Despite this diversity, humans currently satisfy most requirements with surprisingly few plant species; for example, just three crops – rice, wheat and maize – comprise more than 50% of plant derived calories. Here, we synthesize the projected impact of global climatic change on useful plants across the spectrum of plant domestication. We illustrate the demographic, spatial, ecophysiological, chemical, functional, evolutionary and cultural traits that are likely to characterise useful plants and their resilience in the next century. Using this framework, we consider a range of possible pathways for future human use of plants. These are centred on two trade-offs: i) *diversification* versus *specialization* in the range of species we utilize, and ii) *substitution* of the species towards those better suited to future climate versus facilitating *adaptation* in our existing suite of dominant useful plants. In the coming century, major challenges to agriculture and biodiversity will be dominated by increased climatic variation, shifting species ranges, disruption to biotic interactions, nutrient limitation and emerging pests and pathogens. These challenges must be mitigated, whilst enhancing sustainable production to meet the needs of a growing population and a more resource intensive standard of living. With the continued erosion of biodiversity, our future ability to choose among these pathways and trade-offs is likely to be diminished.

**Keywords:** Biodiversity, climate change, conservation, crop breeding, crop wild relatives, domestication, food security, medicinal plants, sustainable development, resilience.

## 1. Introduction

As human population increases and the standard of living improves over the next century, our reliance on the effective and efficient utilisation of plants will grow (Godfray et al., 2010; Guo, Zhang, & Li, 2010). In this review our definition of useful plants follows RBG Kew (2016) in the broadest sense, as "plant species which have been documented as fulfilling a particular need for humans, animals or the wider environment". Of the approximately 400,000 vascular plant species known to science, around 8% (31,000) have documented uses (RBG Kew, 2016), encompassing human and animal foods, fuels, medicines, materials and crop wild relatives, and we note that many more species may be as yet undocumented. While crop plants are perhaps most familiar, more than half of documented useful plants (57%) are used for medicines and twice as many are used for materials (36.5%) than as foods (17.8%) (Farnsworth & Soejarto, 1991; RBG Kew, 2016).

Global biodiversity loss as a result of habitat conversion, overexploitation and climate change is projected to result in a 7-24% decline in vascular plant diversity by 2050 (C. Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Vuuren, Sala, & Pereira, 2006), with climate adaptation becoming a key challenge for many plant species over the next century. The impacts of climate change are predicted to – and in many cases have already been demonstrated to – fundamentally alter several aspects of plant biology including genomic architecture (Ahuja, de Vos, Bones, & Hall, 2010), development (Gray & Brady, 2016), phenology (Springate & Kover, 2014), biotic interactions (Eckert et al., 2010), demography (Miller & Gross, 2011) and distribution (Pecl et al., 2017). This in turn may strongly impact on the quality and yield of the material and non-material products and benefits we derive from them (Challinor et al., 2014; DaMatta, Grandis, Arenque, & Buckeridge, 2010).

An estimated 2,500 plant species from 160 taxonomic families have been altered by human selection in the ~12,000 years since human plant domestication began (Smýkal, Nelson, Berger, & von Wettberg, 2018; Zeven & de Wet, 1982). These species have been subjected to a spectrum of domestication effort (Hammer & Khoshbakht, 2015; Meyer, Duval, & Jensen, 2012; Meyer & Purugganan, 2013), with only around 200 species considered to be extensively domesticated (Meyer

et al., 2012; Vaughan, Balázs, & Heslop-Harrison, 2007), including, for example, extensively engineered crops with annual production measured in the millions of tons (e.g. rice (*Oryza sativa*); Gross and Zhao 2014; Muthayya *et al.* 2014). By contrast, there is a substantially greater number of less extensively utilised species, cultural, shade and ornamental plants, poisons and medicines harvested on a small scale from wild or semi-wild populations (e.g. bamboo shoots (*Bambusa* sp.) in western Thailand, Delang, 2006; Ogle et al., 2003; Schippmann et al., 2002) which have been the subject to little or no human-directed selection (Figure 1). Understanding how climate change will impact these useful plants is critical to developing climate-resilient strategies that are sustainable and continue to derive societal benefits from the plants we depend on. Climate change is a global multi-factor phenomenon which includes increased temperatures, rising $CO_2$ concentrations and UV intensity, as well as changes to the frequency and magnitude of rainfall events, including drought and flooding (IPCC, 2013). Useful plants have been domesticated based on current (or recent past) growing conditions, and in the future, may therefore experience very different conditions than they do today.

Typical features that mark a crop's divergence from a wild ancestor are together termed the 'domestication syndrome' (Harlan, 1971). These often include traits such as seed retention, increased fruit or seed size or palatability, modified nutritive values (including increased protein, fat or sugar content), rapid growth rates, altered reproductive strategy, changes in secondary metabolites, and reduced resource allocation towards non-edible plant tissues as well as pest and pathogen defence (Meyer et al., 2012). Domestication can therefore sometimes work against natural selection, resulting in reduced fitness in a wild setting (Meyer et al., 2012), with knock-on impacts to beneficial insects through changes to floral chemistry that in wild populations supports healthier pollinators (Egan et al., 2018). Given projected future pressures, existing or newly domesticated plants may increasingly be selected for tolerance to climatic variation, nutrient limitation (e.g. increased cost or reduced availability of industrial fertilisers, and/or soil degradation) and emerging pests and pathogens, generating in some cases a novel future 'domestication syndrome'. To better understand these challenges, we explore a representative series of useful plant characteristics that are expected to be

impacted by climate change, from small to large scale (e.g. from genes to geographic distribution) and from intrinsic to extrinsic factors (e.g. from physiological traits to pollination or human cultural preferences). We survey phylogenetic position, geographic distribution, biotic interactions, morphological traits and cultural importance - to consider likely indicators of future success in the context of climate change and human utilization. Importantly, we consider these characteristics across the domestication spectrum, along which is distributed the tremendous global diversity of useful plants, from widely-domesticated crops to rare species harvested from the wild.

We align our review with a range of possible future strategies to meet these challenges (Figure 2). These strategies are characterised by the interaction of two spectra; first, the trade-off between replacing the major species we elect to use to better fit future environmental conditions (*Substitution*) and selecting for improved performance from our existing species (*Adaptation*). Concurrently, society faces a choice between an increasingly narrow suite of highly domesticated species (*Specialization*) or substantially increasing the number of highly utilised species (*Diversification*). Our aim is to stimulate discussion on the likely trajectory for useful plants under climate change as well as highlighting opportunities and trade-offs, whilst better informing the option-values of strategies to sustainably meet the growing human requirements we derive from useful plants.

## 2. The evolutionary history of useful plants

Several studies have investigated the phylogenetic distribution of useful plants, mostly using angiosperm-wide or regional (i.e. flora) phylogenetic trees (Q. C. B. Cronk & Forest, 2017; Saslis-Lagoudakis et al., 2012). Equally, many have explored the potential of phylogenetic trees for the identification of species closely related to plants with chemical compounds of interest (i.e. so-called “bioprospecting”) or crop wild relatives (Ernst et al., 2016; Halse-Gramkow et al., 2016). Fewer studies however have directly addressed the effect, using a phylogenetic framework, that future climate change might have on the conservation and preservation of plants useful for humans (Edwards, Still, & Donoghue, 2007).

### 2.1 The phylogenetic distribution of useful plants

Plants that humans use tend to be phylogenetically clustered (Cronk, 2008; Cronk and Forest, 2017; Meyer and Purugganan, 2013; Moerman, 1991; though see Şerban et al., 2008), and similarly, there is initial evidence that the types of services or products plants provide may also be clustered (Cámara-Leret et al., 2017). Patterns of plant use appear to depend on how common the use is, how common the underlying trait is amongst plant taxa, and how phylogenetically close the taxa are to commonly encountered plants (Cámara-Leret et al., 2017). For instance, a global analysis of plant utilisation showed that common uses are more likely to show phylogenetic clustering than uncommon ones (Dai, Zhang, Xu, Duffy, & Guo, 2017). Conversely, there is also evidence of phylogenetic clustering in plant extinction risk (Forest et al., 2007; Vamosi & Wilson, 2008) suggesting that entire groups of functional traits or uses could be universally vulnerable (Bascompte, Garcia, Ortega, Rezende, & Pironon, 2019).

At the broadest scale, most useful plants are angiosperms (Meyer et al., 2012), although there are some key products derived from other plant groups, in particular from gymnosperms (e.g., pine nuts, timber, medicinal compounds). Highly domesticated food crops show the clearest phylogenetic clustering (Figure 3), however when all food plants (including spices) are considered, Şerban et al. (2008) found little evidence of clustering in the angiosperm tree of life. This study, however, encompasses plants consumed by humanity as a whole; it would be interesting to evaluate the phylogenetic distribution of these species in cultural groups rather than in its entirety. Phylogenetic analyses of useful plants in general have also been limited by lack of documentation on many underutilised species, which is now beginning to be addressed (RBG Kew, 2016).

Most human calories consumed globally are derived from only a handful of crops (e.g., rice, wheat and maize) from the grass family (Poaceae). Within the remaining top 10 families globally utilised for human calorific intake (FAO, 2015), the number of species from the bean family (Fabaceae) are similarly ubiquitous (e.g. globally important soybean or lesser-used groundnuts; Smýkal *et al.* 2014) while the majority of the remaining species dominating the human diet belong to only a handful of

other families such as Solanaceae (nightshades; potatoes), Arecaceae (palms; palm oil) and Asteraceae (daisies; sunflower oil). This bias may reflect both the history of domestication of these taxa (i.e. closely related species may be favoured through cultural experience and familiarity), but also the natural presence of desirable traits among closely related species (i.e. nutritious, low toxicity).

More plant species are used for medicines than for food (RBG Kew, 2016). These plants are more widely dispersed across the plant tree of life, but still tend to show a degree of phylogenetic clustering, likely as a result of complex secondary metabolite pathways that are perhaps less likely to evolve many times independently (Halse-Gramkow et al., 2016; Moerman, 1991). In a study focussing on the plants used in traditional medicine in three distinct regions (New Zealand, Nepal, South Africa), Saslis-Lagoudakis et al., (2012) showed that the medicinal plants of these three floras share phylogenetic patterns, indicating that related plants from the three regions are used to treat similar ailments, which in turn suggests independent discoveries of medicinal properties. Garnatje et al., (2017) termed this 'ethnobotanical convergence' and, where combined with 'omics', suggested that it has the potential to identify new potential applications for plants.

**2.2 Genomic resources for useful plants**

Genomic resources are crucial for effective crop breeding, and the transition of species from underutilised into extensively domesticated crops (or to push them further along the domestication spectrum). Our understanding of the angiosperm phylogenetic tree is being further enhanced and shaped by large-scale phylogenomic projects (e.g. 1KP; Kew's Plant and Fungal Trees of Life; Eiserhardt et al., 2018). The new detailed phylogenetic understanding provided by these programmes is crucial for two main reasons. First to determine the directionality of evolution of particular traits (including their genetic or genomic basis), and secondly to identify the wild relatives of crops, trace in time and space their domestication, and estimate their genetic divergence (Chomicki & Renner, 2014). New and even larger genome sequencing initiatives aimed at sequencing the diversity of underrepresented

plant lineages (e.g. 10KP; Cheng et al., 2018) will help to alleviate the current bias in genomic resources, but they need to be matched by further biological characterisation of these taxa.

Combining such phylogenetic frameworks with ethnobotanical uses (Cámara-Leret et al., 2017) and climatic, trait and usage data (Ernst et al., 2016) will allow more sophisticated predictions of where and how particularly useful traits have evolved across the angiosperm tree of life. Using biological responses to plant extracts rather than standard categories may permit more phylogenetically diverse predictions for bioprospecting, for instance in the medicinally important genus *Euphorbia* (Ernst et al., 2016). Such approaches could permit identification of which species and traits could be used for breeding to tolerate climate change (Mehrabi, Pironon, Kantar, Ramankutty, & Rieseberg, 2019), and in turn, permit the identification of more diverse and unexpected uses for plants than would otherwise have been the case.

The identification of new useful plants may also need to consider the context of hybridisation and ploidy (i.e. cytogenetic information), particularly with accelerated range shifts and species introductions. Many crop plants are polyploids, often allopolyploids (Meyer et al., 2012), the latter resulting from hybridisation between species as well as whole genome duplication (e.g. *Triticum aestivum* – allohexaploid bread wheat; *Solanum tuberosum* – allotetraploid potato). The result is more than two sets of chromosomes with distinctive sub-genomes (from each parental donor). This can result in reproductive isolation from crop wild relatives (which is an important consideration in breeding efforts) but also impacts how species adapt and evolve in response to climate shifts and other ecological factors (Soltis & Soltis, 2016). Genome size itself may also be important to consider given that it ranges c. 2,400-fold across angiosperms, and has been shown to impact both size (e.g. stomatal size, vein diameter) and rate (e.g. duration of mitosis and meiosis) related traits which, in turn, can influence where and how plants grow and respond to environmental change (reviewed in Pellicer et al. 2019).

## 3. The impact of climate change on the distribution of useful plants

### 3.1 The impact across biomes

Climate is a major driver of the spatial distribution of biodiversity (C. Bellard et al., 2012; Hoffmann & Sgró, 2011), exerting a strong influence on the availability of various plants useful to humans around the world. Changing climate is anticipated to result in a significant redistribution of the material and non-material benefits provided by nature (Mooney et al., 2009), though this impact may differ among regions, useful plant species and use types. Boreal and hemi-boreal areas, for example, are expected to experience important climatic modifications with novel and disappearing climates mainly found in north-eastern North America and Asia (Williams, Jackson, & Kutzbach, 2007). Given their relatively poor species richness and endemism in both wild and cultivated useful plants (Pironon et al., *in review*), poleward range extirpations might only affect a relatively limited number of species and potential uses. However, increasing local losses could ultimately lead to global extinctions and, additionally, it could strongly impact the lives of local indigenous populations given their poorer access to replacement options (Garnett et al., 2018). On the other hand, boreal areas represent potential opportunities for the expansion of both wild and domesticated species currently found at lower latitudes (Odgaard et al., 2011, but see also Bebber et al., 2013). Temperate and Mediterranean useful plants may therefore undergo range expansion at higher latitudes, despite declines at their rear-edge. Although rear-edge populations of wild plants may be highly threatened by climate change, they have often persisted under major past climatic fluctuations and contain unique and valuable adaptive genetic diversity (Borrell et al., 2018; Hampe and Petit, 2005). Regions with highly heterogeneous landscapes may facilitate the pursuit of suitable climatic conditions by species at a relatively small scale, and therefore favour their persistence and survival (Ohlemüller et al., 2008). Despite the fact that large negative effects have been observed, climate change tends to impact cultivated plants at a lower intensity in temperate areas, in part because of the higher economic and technological capacity of many countries in these regions (Challinor et al., 2014; Donatelli, Srivastava, Duveiller, Niemeyer, & Fumagalli, 2015; D. B. Lobell & Field, 2007), although well fertilized modern crop varieties seem more sensitive to heat related losses (Schlenker & Lobell, 2010).

The impact of climate change on useful plants may be more severe in the tropics due to generally more persistent food insecurity and a reduced capacity for agricultural adaptation (Muller, Cramer, Hare, & Lotze-Campen, 2011). Large parts of the current tropical climatic space are predicted to disappear together with the emergence of novel climates (C. Bellard et al., 2012; Céline Bellard et al., 2014; Williams et al., 2007). Climate change may more acutely threaten the most important hotspots of useful plants, both in terms of species richness and endemism (Pacifici et al., 2015, Pironon et al., *in review*). Major modern crops such as wheat, maize and rice have been observed to be highly impacted by recent changes in temperature and precipitation regimes in the tropics (Challinor et al., 2014; D. Lobell, Schlenker, & Costa-Roberts, 2011). Mountainous areas are potentially at greater risk in the tropics where species tend to shift their ranges along topographical or habitat features rather than latitude (Rumpf et al., 2018). Moreover, ongoing climate change is outpacing past climatic modifications, which represents a major issue for tropical plants that evolved relatively slowly along elevation (Morueta-Holme et al., 2015; VanDerWal et al., 2012), as opposed to temperate plants that have been exposed to significant range shifts over past glaciations (Qian & Ricklefs, 2016).

There may be benefits to some localized agricultural systems as, for example, the number of cultivable species is observed to increase on the elevational gradient from subtropical lowland to alpine in the Himalayas (Chaudhary & Initiatives, 2016). For species such as coffee, climatically suitable areas are predicted to shift from lowland to higher elevation (Moat et al., 2017), with losses partially compensated by newly emerging climatically suitable areas in Indonesia (Schroth, Läderach, Blackburn Cuero, Neilson, & Bunn, 2015) or Ethiopia (Moat et al., 2017). Overall, cultivation of useful plants is likely to be characterised by accelerated re-distribution of species and agri-systems, with future usefulness of plants potentially favouring those that are easier to transition to new locations or environments, as well as species with lower inputs or better documented indigenous knowledge management requirements. However, for non-cultivated useful plants which represent the largest diversity of species used by human populations, relocation potential seems more limited. Representing a major option value for humans, non-domesticated useful plants will therefore require

strong *in-situ* conservation efforts accounting for species natural dispersal following climate change (Corlett & Westcott, 2013).

**3.2 The impact of range rarity**

Sensitivity to climate change does not only vary among regions (i.e. species range position) but also among species. Species range size represents an important biogeographical feature often related to vulnerability and extinction (Saupe et al., 2015). Under climate change, narrow ranged species are expected to be at high risk due to shrinking habitat and low potential to reach new suitable areas (Ohlemüller et al., 2008). The tropics may be at higher risk due to their expected higher turnover in climatic conditions, and their extremely high concentration of endemic plant species, narrowly-distributed human cultures, and therefore plant uses (Pironon et al., *in review*). Some of the detrimental effects of climate change on useful plants have already been perceived by local communities, such as in the Sierra Nevada del Cocuy-Güicán of Colombia, where climate change, together with unsustainable land use and overharvesting are causing a decline in medicinal plant resources (Rodríguez, Angueyra, Cleef, & Van Andel, 2018). Moreover, narrow-ranged species and tropical areas might be even more vulnerable because they are also expected to be particularly impacted by other global change drivers such as land use change or biotic invasions. On the other hand, wide-ranged species have been demonstrated to have a high adaptability to changes in climatic conditions (Newbold et al., 2016), even though many wild plants might not be able to expand quickly due to dispersal lag (Svenning et al., 2008). It is also important here to note that the ecological niche occupied by a species will also affect its ability to adapt to climate change, and that this might be uncorrelated to its geographic range (i.e. a species with a large distribution range could more easily be obliterated should it have a narrow ecological niche). For example, wetland rice, which is cultivated globally, is more vulnerable to heat stress by climate change compared with other key crops (Teixeira, Fischer, Velthuizen, Walter, & Ewert, 2013).

Overall, in this context, useful plants might suffer relatively less from extinction than other wild plants as the geographical ranges of many have been largely expanded and intensified by humans through some level of domestication, breeding, agricultural practices, global trade, or accidental introduction (Coradin et al., 2018; Dempewolf et al., 2014; Khoury et al., 2014; Khoury et al., 2016). Future manipulation of useful plant distributions – and mitigation of negative climate change repercussions on plant derived benefits – will be dependent on accurate climate projections enabling identification of appropriate species and areas to utilise or cultivate across the landscape (Pironon et al., *accepted*). As a result, underutilized narrow-range or narrow-niche plants might represent important targets for short-term conservation actions (Padulosi, Heywood, Hunter, & Jarvis, 2011), perhaps through domestication.

## 4. The impact of climate change on biotic interactions with useful plants

A large proportion of plants, including those useful to humans, depend on biotic interactions for pollination, predation of pest herbivores, seed dispersal, or persist where herbivores or harmful pest and pathogens do not. Here, we predominantly consider insect interactions relating to pollination and pests, as these are among the most extensively researched, though we note the importance of interactions between pests and pathogens, seed dispersers, rhizobial symbionts and mycorrhizal associations. Evidence about how climate change influences plant-insect interactions is growing and indicates that these changes can have a negative impact, notably for pollination (Eckert et al., 2010) and beneficial tri-trophic interactions such as those provided by natural pest regulation (Dyer, Richards, Short, & Dodson, 2013), but may also exacerbate the occurrence of pests (Deutsch, Tewksbury, & Tigchelaar, 2018).

### 4.1 The impact on plant-pollinator interactions

Outcomes for pollination include increased selection for selfing and perennialism (Otto, 2018), reduced phenological and distributional overlap between plants and their pollinators, and decreased variety in forage for pollinators (Memmott, Craze, Waser, & Price, 2007; Solga, Harmon, & Ganguli,

2014). *In extremis* the outcome may be the extinction of pollinators, plants or their interactions (Bascompte et al., 2019; Memmott et al., 2007). The consequences of changing climate on pollinators may not be fully apparent for decades (Burton & Lim, 2005) although severe discrete effects appear likely in some circumstances (Garibaldi et al., 2016). While responses by plants and pollinators to increasing temperature may occur concurrently, there is considerable variation in the direction and magnitude of the response (Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009) suggesting potential spatial and temporal mismatch. For example, plants may flower earlier with increasing temperature (Fitter & Fitter, 2002; Penuelas, 2002) but first emergence of pollinators may be slower to respond (Gordo & Sanz, 2005; Hegland et al., 2009), and the success of pollination services is highly dependent on synchrony between flower and pollinator. This is particularly apparent in highly specific pollinator plant interactions. The first flight date of the solitary bee *Andrena nigroaenea* advances more in response to higher temperatures than the flowering date of the orchid *Ophrys sphegodes*, which *A. nigroaenea* males inadvertently pollinate through pseudocopulation owing to the flower mimicking the odour and appearance of the female bee (Ayasse et al., 2000). Ironically, advanced emergence of both genders leads to greater competition for males by female bees with the plant losing out. Small temperature rises increase the probability of males and females flying at the same time and before orchid flowering, reducing the frequency of pseudocopulation and pollination success for the flower (Robbirt, Roberts, Hutchings, & Davy, 2014).

Pollinator ranges are also fluctuating, in some cases characterized by migration to cooler latitudes and higher altitudes, although these changes are not always compensated at opposing range limits (Potts et al., 2016). For example, in 67 bumble bee species across Europe and North America, southward range contractions of up to 300 km have been recorded compared to historical distributions, with closely related species showing similar shifts – yet typically the northward range expansions are limited by availability of forage, particularly for oligolectic species and specialists since plant range expansions are too slow. This results in an overall range contraction with potential temporal and spatial mismatches for plants dependent on these pollinators (Bascompte et al., 2019; Kerr et al.,

2015). Changing pollinator ranges could lead to a loss in pollinator diversity or abundance leading to lower food production (Potts et al., 2016). Seasonal behaviour and ranges of many pollinators may change but differentially, leading to disruption of life cycles, plant-pollinator interactions and population structure and composition (Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008). Different groups of pollinators may be too slow to adapt to rapid temperature changes disrupting crop pollination especially if the overlap of climatic conditions for crops and their pollinators is limited (Giannini et al., 2013; Polce et al., 2014; Settele et al., 2016).

The combined and interactive effects of different stressors (e.g. pesticide exposure, diseases, habitat loss and climate change) for pollinators are also predicted to be important (Vanbergen et al., 2013). Thus, the likely consequences of multiple interacting factors such as habitat loss exacerbated by climate change may lead to greater impacts on pollination services by limiting capacity to compensate for range shifts (Thorne et al., 2010). This may lead to landscapes dominated by adaptable generalists at the expense of less adaptable specialists (Settele et al., 2016), with consequences for plants with specialist pollinator syndromes. For example, butterfly species that were mobile and habitat generalists increased in distribution consistent with exploiting warmer temperatures, whereas less motile generalists and habitat specialists declined in distribution consistent with being limited by habitat loss (T. Warren, 2001). So, the combined effects of landscape and climate may cause specialists to decline, reducing population diversity and placing plant species at risk.

Changes to climate other than temperature may also detrimentally impact biotic interactions. Cocoa production for example is uniquely dependent upon the pollination services of Ceratopogonid midges (Bogdanski et al., 2008). There is increasing evidence that pollinator limitation (Forbes and Northfield, 2015; Groeneveld et al., 2010) is influenced by drought rather than temperature since the lifecycle of the pollinator relies on high forest floor moisture for larval development (Arnold et al., 2018). It is possible that similar impacts may manifest themselves in wild populations of *Theobroma* species influencing future diversification within the genus, since it shows greater diversity at lower altitudes

that may be warmer and wetter (Richardson, Whitlock, Meerow, & Madriñán, 2015) and changes to this status may influence diversity and abundance of pollinators and their services in different habitats.

**4.2 The impact on pest regulation**

Trophic interactions where beneficial invertebrates provide natural pest regulation may also be affected, particularly since the natural enemies of many pests also rely on non-crop habitats for food, refuge and as alternative hosts (Gurr, Wratten, Landis, & You, 2016). However, by comparison to pollinators much less is reported about natural enemies of pests. Dyer et al. (2013), for example, report that higher temperatures and $CO_2$ concentrations led to developmental asynchrony between the parasitic wasp *Cotesia marginiventris* and its host, the larvae of the moth *Spodoptera exigua*, and in some cases, to the mortality of the wasp. More recently, Roslin et al., (2017) reported that insect predation increases towards the Equator and lower elevations suggesting a strong association with higher temperature which may influence the range and effectiveness of natural regulation of pests with consequences for crop production. Thus, natural pest regulation that is dependent on insect predators or parasitism may decline as a direct consequence of a changing climate, which could particularly impact plants that have been domesticated and are now cultivated at large scales.

Climate may also influence the severity and temporal phenology of herbivory that may result in major consequences for useful plants. This is particularly so for domesticated species that have been bred for uniform traits so are more susceptible to major outbreaks of insects. For example, the tent caterpillar *Malacosoma disstria is* a major pest of poplar and birch trees, which have regional importance for silviculture. However an increase in temperature of between 1.7 and 3.4°C has resulted in more advanced spring phenology for trees than insects, potentially mitigating against risks of major outbreaks (Schwartzberg et al., 2014). Conversely, models evaluating relationships between temperature, population growth and metabolic rates in insects show that global increases in

temperature could lead to an escalation in preharvest losses of rice, maize, and wheat with increases estimated to be up to 25% per degree of temperature increase (Deutsch et al., 2018).

### 4.3 Generalism vs specialism in biotic interactions

In the future, the effective and efficient use of plants in food production, provisioning and supporting ecosystem services may increasingly depend on the discovery and conservation of other related species for which plant pollinator interactions are less affected by climate change. Alternatively, continued management of useful plants may also extend to the network of species with which they interact. Concurrently, there may be increasing demand for plant species less reliant on pollinators and plant selection favouring selfing or clonal reproduction. This may be the case, for example, with *Theobroma* species (cacao) for which selfing is an alternative pollination system although with poorer yield and higher risk of fruit abortion (J. Warren, Misir, & Kalai, 1995). While current concerns focus primarily on short-term impacts, climate change has disrupted ecosystems and trophic interactions over much greater time scales affecting abundance and ranges leading to communities dominated by generalists (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013). Understanding how climate influences trophic interactions and community dynamics will be critical to predicting how managed and unmanaged ecosystems react to change in the short and longer term, and crucially could involve cases where rapid evolution alters provision of ecosystem services (*sensu lato* Rudman et al., 2017).

## 5. The future of useful plant traits

In the future, useful plants are very likely to be growing in different conditions than they are today, either through inability to track their climate envelope, reduction or disappearance of their historical climate niche (see section 4) or reluctance or inability of users to shift to new species. Projected changes will include warmer temperatures, more frequent drought or flooding, increased UV exposure and rising $CO_2$ concentrations (IPCC, 2013; Figure 4). Concurrently, there may be agricultural pressures to reduce energy intensive or environmentally harmful inputs such as fertilizers and pesticides. The interactions of these environmental variables with plant traits is complex and the traits

which best promote resistance and resilience to climate change will be strongly context and scale dependent. There are two general strategies to enable plant resilience to climate change: i) selecting for positive adaptive traits to a given abiotic stress or ii) selecting for traits to avoid a particular stress factor (e.g. increased seed dormancy or changes to phenology). The appropriate strategy in any given situation is likely to be dependent on the duration, direction and magnitude of projected climatic changes, as well as the resource allocation and morphological trade-off with other desirable plant traits.

Plants can also alter the environment they are exposed to through 'niche construction' mechanisms (*sensu* Laland et al., 2016), such as phenology, seed dispersal, dormancy and germination (Donohue, 2005). Domestication has directly or indirectly influenced many of these traits (i.e. "human driven niche construction" (*sensu* Smith, 2007) with seed traits that had been of selective advantage for wild seed-bearing plants, including seed dormancy, not necessarily being advantageous for crops. These differences in functional seed traits might, for example, limit the capacity of cultivated plants to cope with periods of drought in contrast to their wild relatives (e.g. Castillo-Lorenzo et al., 2019; Castillo-Lorenzo et al., 2018).

We emphasise that whilst many trait shifts in response to climate change may be negative, or erode plant usefulness, some aspects of future climate, such as elevated $CO_2$ levels, may present opportunities for increased yield or value. Finally, whilst we principally consider adaptation involving genetic change in this manuscript, acclimatization (i.e. phenotypic plasticity) may also facilitate adaptation, though this ultimately has a genetic basis.

**5.1 Adaptation to changing precipitation**

The direction of precipitation changes, either increasing or decreasing, is likely to be spatially variable, with the frequency and magnitude of droughts expected to increase across many regions. Plant traits that promote drought tolerance fall into two categories; water saving and water acquisition traits. Water saving traits include a shorter habit, smaller leaves, early maturity, plasticity in leaf chemistry

for osmotic control and the capacity for prolonged stomatal closure which reduces seasonal evapotranspiration (Cattivelli et al., 2008). Increased investment in roots as well as deeper, finer roots, rather than shallow tap roots, promotes water acquisition when water is scarce (Fry, Evans, Sturrock, Bullock, & Bardgett, 2018). Conversely, other regions will be exposed to more frequent and severe flooding. The ability to maintain high levels of soluble sugars in plant tissues during germination is one proposed mechanism for tolerance to fresh water (Peña-Fronteras et al., 2009) and salt water flooding (Colmer, Vos, & Pedersen, 2009). Traits associated with the rapid closure of root stomata, larger interconnected aerenchyma that allows oxygen translocation and rapid petiole elongation also confer flood tolerance in addition to traits that support seed dormancy under anoxic conditions (Else, Janowiak, Atkinson, & Jackson, 2009).

**5.2 Adaptation to increased temperature and $CO_2$ levels**

Unlike precipitation, both temperatures and $CO_2$ concentrations are expected to rise across most regions, although this will vary in magnitude (IPCC 2013). Smaller, fibrous and slow-growing leaves with thicker cell walls, narrowly spaced veins, greater hair densities and high lignin content are generally associated with heat tolerance (Kering, Guretzky, Funderburg, & Mosali, 2011). However, these traits are generally undesirable in human food crops and, in animal feed, can lead to increased enteric methane emissions (Lee, Davis, Chagunda, & Manning, 2017). Other traits, such as a greater photosynthetic rates, increased membrane thermostability (e.g. cellular lipids and/or sugars) and the maintenance of RUBISCO production may confer heat tolerance in a way which does not limit yields (Larkindale & Huang, 2004). Synthesis of some of the intra-cellular compounds which protect plant tissues from heat may also protect them from UV damage (Wahid, Gelani, Ashraf, & Foolad, 2007). An example is the production of anthocyanins in leaves and fruits, the consumption of which may also offer human health benefits (Cassidy, 2018). Rising temperatures may lead to increased productivity in some cases and $CO_2$ can also have a fertilising effect on plants. Yet this effect is not universal and often becomes saturated even at relatively low $CO_2$ concentrations (M. Lee, Manning, Rist, Power, &

Marsh, 2010). Traits which promote a continued $CO_2$ fertilisation effect as concentrations increase may therefore be beneficial and include greater photosynthetic nitrogen use efficiency, a high relative growth rate (particularly of meristems) and an ability to maintain a consistent partitioning coefficient, with plants investing an equal proportion of the additional energy into photosynthetic capacity (e.g. increased number or surface area of leaves) and product (e.g. increased number or mass of seeds) (Bishop, Betzelberger, Long, & Ainsworth, 2015; Oguchi, Ozaki, Hanada, & Hikosaka, 2016).

**5.3 Adaptation in nutritional and chemical traits**

Changes in precipitation, temperature and $CO_2$ levels have been shown to influence chemical composition across a diverse range of useful plants (Holopainen et al., 2018; Hummel et al., 2018; Loladze, 2014). These changes could have a substantial impact on the benefits derived from certain species, relevant to their uses for nutrition, as medicines and other uses for humanity. For example, Laenoi et al., (2018) showed that in four modern varieties of rice, both yield and grain quality responded differently across seasons and in general had lower concentrations of nutrients including N, P, Fe and Zn in the wet season. Similarly, exposure to UVB light, which is predicted to increase with climate change, can negatively affect the nutritional quality of certain soya bean cultivars (Choudhary & Agrawal, 2015). As atmospheric $CO_2$ rises, plants are predicted to have increased starch and reduced protein content, which is associated with a decline in digestibility (Ziska, Epstein, & Schlesinger, 2009). Indeed, increased $CO_2$ leads not only to decreased protein, but also reduced levels of iron and zinc in crops such as wheat, rice, potatoes, soy, and peas, and in fruits and vegetables, which are important sources of nutrients especially in many low-income countries (Fanzo, Davis, McLaren, & Choufani, 2018; Green et al., 2018). Conversely, some studies conclude that elevated $CO_2$ levels can increase grain (including wheat and canola) yield, which is an important factor to support livelihoods. The negative effect on grain nutritional value is, however, likely to have long term consequences for human health (Jin, Armstrong, & Tang, 2019). Furthermore, abiotic stresses including light, temperature, drought and altered soil composition that may be linked with climate change have

already been shown to have a negative impact on the nutritional value of forage crops, affecting livestock health (Kulkarni et al., 2018). Ozone ($O_3$) is a contributor to climate change and it reduced the nutritive quality of forage crops including ryegrass (*Lolium perenne*) and clover (*Trifolium subterraneum*) (Kulkarni et al., 2018). Thus, from the emerging evidence available to date, climate change could mean higher yields of less nutritious crops with consequences for both human and livestock health.

There is, however, evidence to suggest that extreme environmental conditions may increase production of certain secondary metabolites in plants in response to stress factors, such as flavonoids in vegetables, and phenolics with antioxidant activity in quinoa (Dong, Gruda, Lam, Li, & Duan, 2018). Such compounds may be produced by plants in response to environmental stressors, but are also relevant to maintaining human health beyond functional nutrition (Howes & Simmonds, 2014). Plant secondary metabolites not only provide benefits to human health by maintaining a dietary range, but their increased production could have relevance to the medicinal or social uses of plants and their chemical constituents. For example, higher $CO_2$ can increase morphine production in the wild poppy (*Papaver setigerum*) and digoxin production in *Digitalis lanata* (Ziska et al., 2009). Increased yields of such pharmaceutically important compounds may be useful to meet therapeutic demands in the future, but levels of other secondary metabolites with toxic or other potentially adverse effects (e.g. allergens) may also be increased, with consequences for the value of currently useful plants and for human health.

**5.4 Adaptations in seed germination biology**

Climate change is altering the drivers for seed dormancy and germination, and in the future may preclude, delay, or enhance regeneration from seeds (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). As a result, there is no clear positive or negative response in useful plants and we cannot predict whether emergence will continue to match with the season favourable for establishment (Fernández-Pascual, Mattana, & Pritchard, 2018). Breaking dormancy and germination are complex physiological

events. The more developmental stages from imbibition to germination, the increasing likelihood that changes in the environment could affect or disrupt reproduction by seeds. For example, seeds with morphophysiological dormancy could have different thermal thresholds for the internal growth of the embryo and radicle protrusion. This appears to be the case for some species with rudimentary embryos in Ranunculaceae (Porceddu, Mattana, Pritchard, & Bacchetta, 2017). Wild plants show a high intraspecific variation in traits underpinning seedling emergence, growth and establishment (Cochrane, Yates, Hoyle, & Nicotra, 2015). However, it is not yet possible to make generalizations about how this variation is allocated across geographic ranges and further research to identify the distribution of seed traits within foundation species and the mechanisms driving them is required (Cochrane et al., 2015). In wild populations of useful plants, persistence in the soil seed bank may be affected by the abiotic environment (Long et al., 2015). Warmer soil can increase seed bank decay due to increased germination rates, for facultative pyrogenic plants, whose physical seed dormancy (i.e., seeds with an impermeable coat) is broken by high temperature thresholds (Ooi, Denham, Santana, & Auld, 2014).

**5.5 Selection of life history traits**

The time taken to domesticate crops has decreased since the earliest domestication events (Meyer et al., 2012; Vaughan et al., 2007), suggesting that accelerating the development of certain traits in underutilized plants is possible. Similarly the processes and timing leading to domestication can vary across groups of plants, depending especially on how they are reproduced – by seed or vegetatively by cuttings – as well as which plant part is being selected for (Fuller et al., 2014). Trees and longer-lived plants, for example, have historically been domesticated at a slower rate than annuals with shorter life cycles, due to extended juvenile stages which delay the point at which desirable (often reproductive) traits can be evaluated and selected. This in turn means that perennial crops often retain higher genetic diversity than annual crops (Miller & Gross, 2011). Therefore, if we sought to accelerate the domestication of underutilized species, on the one hand we may prefer to focus on shorter

lifecycle species, i.e. annuals. Yet conversely, whilst the majority of annual crops are grown from seed, more than 75% of perennial crops are clonally propagated, which overcomes the challenges of a long juvenile stage and eliminates the variation of sexual reproduction (Miller & Gross, 2011). Whilst annuals predominate in our current food system (McClure, Sawler, Gardner, Money, & Myles, 2014), from a plant domestication perspective, it is not yet clear which life history traits will be most advantageous in the future.

**5.6 Multi-trait adaptation**

Climate change is multifactorial, therefore traits that confer resistance or resilience to multiple climatic effects (whilst simultaneously retaining traits for enhanced production and nutrition) would be preferable. For example, reaching maturity earlier in the season, flowering at cooler times of the day, expression of protective secondary metabolites which offer osmotic control, and deeper, finer roots may offer combined protection against warming, drought and UV (Shah et al., 2011). If flooding is projected, then traits which promote additional growth, phenological shifts or dormancy in adverse, often anoxic, conditions will be favourable. The interactions between different climatic variables can also lead to synergistic or antagonistic effects on useful plants. For example, it is known that simultaneously increasing rainfall and nitrogen enrichment can increase plant productivity to a greater degree than the sum of their separate effects, since the additional water washes the dissolved nitrogen over roots, aiding nutrient uptake (Lee et al., 2010). The interactive effects of $CO_2$ with warming or drought varies substantially between plant species and can be synergistic, antagonistic or neutral, with additional complexity added since the outcome can be further modified by factors such as phenological stage, intensity and stress duration (Kadam et al., 2014).

Given the complexities associated to the prediction of future climates for a given location, particularly at a finer-scale, combined with inter-annual variation in conditions, then it may be preferable to cultivate multiple genotypes with different traits as an insurance against different climatic outcomes. Concurrently, many traits will be linked and therefore the selection of some traits will automatically

cause a rise or trade-offs in other traits (Díaz et al., 2016), thus a more thorough understanding of linked traits will be required for breeding optimisation. It will be important to consider the direction, magnitude and likelihood of multiple aspects of climate change and the full suite of plant traits if we are to adequately adapt to our changing world. Technical advances, such as genomic selection or prediction, which uses genome-wide markers to predict individual's breeding values, may permit selection for multiple traits whilst maintaining genetic diversity (Crossa et al., 2017).

## 6. The cultural influences on our use of plants

Although agriculture began up to 12,000 years ago (Meyer & Purugganan, 2013), in many parts of the world people have continued to exploit seasonally available food sources from the wild. Domestications occurred independently on different continents within different temporal contexts, and the possible climatic and socio-economic reasons are still debated, along with the co-evolutionary mechanisms behind these recurrent parallel processes (Fuller et al., 2014). Change accelerated dramatically in the mid-twentieth century with the green revolution focusing on increasing yields of a small number of species. This was accompanied by new farming practises with high use of fertilizers and agrochemicals, altered irrigation techniques (Pingali, 2012), and accelerated cultural selection of a smaller suite of focal useful plants (Meyer et al., 2012). More recently, this trend has been countered by efforts to increase the number of crops and foster the conservation and sustainable use of the whole biodiversity portfolio for human use. For example the FAO Commission on Genetic Resources for Food and Agriculture recently recognised the value of "Globally Important Agricultural Heritage Systems" (FAO 2018), which are traditional systems with high agrobiodiversity, resilient ecosystems, and linkage of farming practices to cultural identity and local ecological knowledge (e.g. the Ethiopian Highlands; Borrell et al., 2018). Other initiatives that have gained traction include the African Orphan Crops Consortium (http://africanorphancrops.org), The Millennium Seed Bank (MSB) in the UK, supported by a global network of partner institutions, and The Global Crop Diversity Trust's Svalbard

Global Seed Vault in Norway to safeguard through duplicate storage as much of the world's unique crop genetic material as possible (Ulian, Pritchard, Cockel, & Mattana, 2019).

**6.1 Transitions between major and minor useful plants**

The plants a community or society may choose to cultivate or harvest from the wild may be strongly influenced by climate and biogeography, but these factors also interact with technological developments, socio-economic changes and cultural preferences. Many crops that are currently 'minor' have been major crops or had wider distributions in the recent or ancient past (Austin, 2006). Species use may change for many reasons, including shifts to more beneficial alternative species, as a result of overharvesting (Parejko, 2003), changes in their major use preference (i.e. food to construction, fodder to medicine) or the development of new uses for existing crops (e.g. grain crops adapted for biofuel production) (Hill, 2007). In northern Sudan, several indigenous African crops including sorghum, lablab and cowpea, were major crops until recently, but have become less important (Ryan, 2018). Lablab (*Lablab purpureus*) in particular has been described as a 'lost crop' in Africa, yet in India, lablab still has considerable importance, showing spatial variation in societal value of crops even outside of their regions of origin. This demonstrates that whilst there has been a decline and homogenisation of global plant species utilization, it is possible for currently minor species to become more widely utilized once again. Some species have been exploited for other purposes, before being additionally used for food (Meyer et al., 2012). For example *Theobroma cacao*, now used worldwide to produce chocolate, was originally used in the production of a fermented beverage and is still used for preparing *mole* in Mexico, whilst others can lose some of their applications, for example more palatable and easier to process enset landraces may be less suited to fibre production (Borrell, Biswas, et al., 2018).

**6.2 Human influence on plant resilience**

There are several strategies to facilitate climate adaptation whilst continuing to derive material and non-material benefits from useful plants. In the short-term, the conservation of extant genetic

diversity, particularly in a period of rapid environmental change, is critical to enable future crop development. Human selection for useful plant traits is sometimes at odds with natural selection of fitness traits; thus maintaining diversity across all traits, not just target traits, is considered important (Fu, 2015). For the majority of useful plants that are not cultivated, cultural choices are crucial to enable conservation of wild populations. Conservation may also be key to enabling discovery of currently unknown or undocumented useful plants (Dempewolf et al., 2014; Garnett et al., 2018; Rodríguez et al., 2018). In the medium-term, plant breeding and genomic prediction tools are likely to enable faster development of resilience traits (for example; breeding of dieback resilient *Fraxinus* in the UK). Concurrently, for wild populations, assisted gene flow or migration strategies could be employed to facilitate adaptation (Aitken & Bemmels, 2016).

In the longer term, *ex situ* conservation strategies for preservation of genetic resources from useful plants will need to be adapted to the effects of climate change on certain seed traits and be mindful of how these traits are represented in the range of species considered as useful plants. For example, seed storability has been a key trait selected during crop domestication. Indeed, 84% of the world´s major crops or crop complexes listed in Annex I of the International Treaty for Plant Genetic Resources for Food and Agriculture produce seeds that are considered orthodox (i.e. tolerate desiccation and storage at low temperatures, the standard seed storage conditions) and these seeds can be stored *ex situ* for relatively long-periods of time (Pritchard, 2016). However, seed storability (i.e. desiccation tolerance and longevity) is affected by changes to the parental environments, and the environmental conditions expected under climate change scenarios may potentially reduce seed storability for diverse species (Kochanek, Buckley, Probert, Adkins, & Steadman, 2010). Additionally, there is an increasing number of plant species that are or have the potential to become useful plants for which seed storability may be reduced or intractable using the standard seed storage conditions (i.e. recalcitrant seeds that do not tolerate desiccation and/or storage at low temperatures and clonally reproduced crops) (Li & Pritchard, 2009). This is particularly important in the tropics where there is the largest concentration of recalcitrant seeded species (Wyse & Dickie, 2017). Historically,

recalcitrant seeds (desiccation intolerant) and clonally reproduced crops have required field gene banks and *in vitro* collections. These methods are higher risk as, for example, field gene banks are exposed to pests and the unfavourable environmental changes predicted under climate change. New approaches such as Cryobiotechnology, including cryogenic storage and explant recovery *in vitro* (Pritchard, 2018), provide a long-term solution for previously intractable species and is also likely to improve longevity of orthodox seeded species (Walters, Wheeler, & Stanwood, 2004).

Finally, we note that genetic engineering is likely to play an increasingly important and sophisticated role in manipulating the diversity of useful plants. In the short term, this is likely to benefit a relatively narrow range of extensively domesticated (and better studied) species, and in the context of this review could be considered a form of *Adaptation-Specialization* (Figure 1). A full discussion of this broad topic is outside of the scope of this review, and we refer the reader to Ortiz et al., (2014).

**6.3 Preservation of indigenous knowledge associated with useful plants**

The efficient exploitation of many underutilised useful plants depends to a large degree upon the preservation of associated, and often diverse indigenous knowledge, for example the complex cultivation and processing practices for enset in Ethiopia (Borrell et al., 2018). It is important to recognise that many communities still cultivate relatively few species, and are reliant on harvested (wild) plants for construction, medicine, tools, food, firewood (and also game animals dependent on plants) (Mollel, Fischer, Hemp, & Fischer, 2017). Indigenous knowledge combined with science has been suggested as one of the most effective approaches to achieving agricultural climate adaptation (Makondo & Thomas, 2018). There is increasing evidence that a large proportion of this knowledge is endangered, with the future of many underutilised plants depending upon addressing cultural biases against the use of local or traditional food crops (Berkes, Colding, & Folke, 2000; Makondo & Thomas, 2018). For example modernising cultural attitudes see some traditional wild harvested plants as ‘children’s food’, or indigenous species are overlooked because they are perceived as ‘backwards’ in favour of introduced ‘modern’ crops (Yemataw, Tesfaye, Zeberga, & Blomme, 2016).

### 6.4. Useful plants as an option value

Conservation of species and ecosystems is essential to preserve useful plant diversity but is inhibited by the scale of the challenge and limited resources. In this regard, phylogenetic diversity (which in many cases may also be spatially correlated with biodiversity hotspots) has been considered as a suitable representative of feature diversity (but see Kelly et al., 2014 and Owen et al., 2019 for further discussion of this topic). Consequently, maximizing phylogenetic diversity would be an efficient way to identify potential future value of plant diversity, including plants useful to humans (i.e. the concept of option values; Faith, 1992). In the future, the desire to create sustainable products will require new solutions to overcome the overexploitation of wild raw resources. New challenges (e.g. reduction in single use plastics, emerging diseases) may also require development of entirely new classes of useful plant product, from as yet unexploited branches of the plant tree of life.

## 7. Conclusion

Useful plants underpin human well-being and the global economy, but the majority are under-documented and under-developed. Lack of knowledge on the ecological characteristics of many useful plant species emphasises the urgent need to synthesise the future impact of climate change on our useful plant resource system over the next century. In this review we have identified a range of characteristics that may be typical of the useful plants we will increasingly rely on in the future as well as conceivable pathways for society's use of plants (Figure 2).

Different combinations of characteristics or traits are likely to be favoured under different pathways. A trend towards *adaptation*, for example, may intensify the pattern of domestication that is already established, with continued emphasis on our existing extensively domesticated species. This would be concomitant with development of novel genomic and breeding approaches to make further performance gains whilst technological solutions may also be sought for pest regulation, plant-pollinator interactions and appropriate irrigation or nutrient inputs. Conversely, *substitution* may favour different species, better suited to future conditions – i.e. useful plants that already display

desired traits to tolerate climate change – but in which productivity traits may not yet have been extensively developed. In this case, useful plant development may focus on species with higher temperature tolerance, improved photosynthesis and water use efficiency. The key difference between *adaptation* and *substitution* is that the former relies on technology to develop traits in species with existing desirable yield or product attributes, enabling them to tolerate future climatic conditions, whereas *substitution* favours species already (or likely to be) tolerant of future climatic conditions, with development of 'useful' features or traits being secondary.

Concurrently, a trend towards specialization is likely to favour wide-spread generalist species, selected to be tolerant to a wide range of climatic conditions. They may have more generalist pollinators (or no pollinator), and a range of uses or co-products enabling multiple benefits to be derived from a limited pool of species. It is likely that many of the species used under a specialization scenario are already moderately or extensively domesticated, though some may be subject to reduced intra-specific diversity. The alternative trend, *diversification*, entails increasing use of larger numbers of species. A key pillar to support this trend would be conservation, to support maintenance of option values, particularly in species-rich areas such as the tropics. Conservation of crop and crop wild relative genetic diversity would be prioritized, together with accelerated documentation of indigenous knowledge associated with weakly domesticated or wild harvested species. From a phylogenetic perspective, a better understanding of the frequency of different uses across and within plant families would aid management of useful plant resources, as well as facilitate the identification of novel useful plants.

The strategies considered here are a simplified representation of a continuous spectrum of pathways and a subset of useful plant characteristics. These pathways should be framed by the current global trend towards lower numbers of species and reduced genetic diversity. Therefore, on our current trajectory, without adequate *in situ* and *ex situ* conservation of species and genetic diversity, the *adaptation* and *specialization* pathways become increasingly unavoidable. Conservation and seed

banking interventions, now, could help ensure that the full range of pathways are available in the future. In the near term, global and national agricultural and conservation policies will substantially influence society's long-term trajectory across these spectra of strategies. Useful plant documentation efforts, for example, should be a priority in the same way that seed banks have sought to safeguard physical plant diversity. Similarly, robust multilateral systems of access and benefit-sharing will be critical to ensure equitable benefit from useful plants, and are key to enabling strategies such as *substitution* and *diversification*. We conclude that whilst we currently have a choice of strategies, the continued loss of diversity combined with climate change means that without effective safeguards and planning, the range of strategies available to us will become much more limited.

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## Contributions

JB and SP conceived and edited the manuscript. All authors contributed to the writing of the manuscript. All authors approved the final version of the manuscript.

## Declarations of interest

None

**Author statement**

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## References


Ahuja, I., de Vos, R. C. H., Bones, A. M., & Hall, R. D. (2010). Plant molecular stress responses face climate change. *Trends in Plant Science*, *15*(12), 664–674. https://doi.org/10.1016/j.tplants.2010.08.002

Aitken, S. N., & Bemmels, J. B. (2016). Time to get moving: Assisted gene flow of forest trees. *Evolutionary Applications*, *9*(1), 271–290. https://doi.org/10.1111/eva.12293

Arnold, S. E. J., Bridgemohan, P., Perry, G. B., Spinelli, G. R., Pierre, B., Murray, F., … Stevenson, P. C. (2018). The significance of climate in the pollinator dynamics of a tropical agroforestry system. *Agriculture, Ecosystems and Environment*, *254*(November 2017), 1–9. https://doi.org/10.1016/j.agee.2017.11.013

Austin, D. F. (2006). Fox-tail Millets (Setaria: Poaceae)—Abandoned Food in Two Hemispheres. *Economic Botany*, *60*(2), 143–158. https://doi.org/10.1663/0013-0001(2006)60[143:fmspfi]2.0.co;2

Ayasse, M., Löfstedt, C., Ibarra, F., Schiestl, F. P., Francke, W., Hansson, B., & Paulus, H. F. (2000). Evolution of Reproductive Strategies in the Sexually Deceptive Orchid Ophrys Sphegodes: How Does Flower-Specific Variation of Odor Signals Influence Reproductive Success? *Evolution*, *54*(6), 1995–2006. https://doi.org/10.1554/0014-3820(2000)054[1995:eorsit]2.0.co;2

Bascompte, J., Garcia, M. B., Ortega, R., Rezende, E. L., & Pironon, S. (2019). Mutualistic interactions reshuffle the effects of climate change on plants across the tree of life. *Science Advances*.

Bebber, D. P., Ramotowski, M. A. T., & Gurr, S. J. (2013). Crop pests and pathogens move polewards in a warming world. *Nature Climate Change*, *3*(11), 985–988. https://doi.org/10.1038/nclimate1990

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of Climate Change on the Future of Biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x.Impacts

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014). Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography*, *23*(12), 1376–1386. https://doi.org/10.1111/geb.12228

Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of Traditional Ecological Knowledge as Adaptive Management. *Ecological Applications*, *10*(5), 1251–1262.

Bishop, K. A., Betzelberger, A. M., Long, S. P., & Ainsworth, E. A. (2015). Is there potential to adapt soybean (Glycine max Merr.) to future [CO2]? An analysis of the yield response of 18 genotypes in free-air CO2 enrichment. *Plant, Cell and Environment*, *38*(9), 1765–1774. https://doi.org/10.1111/pce.12443

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science*, *341*(August), 499–504. https://doi.org/10.1126/science.1237184

Bogdanski, A. K., Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T., Bos, M. M., Veddeler, D., & Tylianakis, J. M. (2008). Caveats To Quantifying Ecosystem Services: Fruit Abortion Blurs Benefits From Crop Pollination. *Ecological Applications*, *17*(6), 1841–1849. https://doi.org/10.1890/06-

1763.1

Borrell, J. S., Biswas, M. K., Goodwin, M., Blomme, G., Schwarzacher, T., Heslop-Harrison, P. J. S., … Wilkin, P. (2018). Enset in Ethiopia: a poorly characterised but resilient starch staple. *Annals of Botany*, *xx–xxx*, 1–20. https://doi.org/10.1093/aob/mcy214

Borrell, J. S., Wang, N., Nichols, R. A., & Buggs, R. J. A. (2018). Genetic diversity maintained among fragmented populations of a tree undergoing range contraction. *Heredity*, *121*, 304–318. https://doi.org/10.1038/s41437-018-0132-8

Burton, I., & Lim, B. (2005). Achieving adequate adaptation in agriculture. *Increasing Climate Variability and Change: Reducing the Vulnerability of Agriculture and Forestry*, 191–200. https://doi.org/10.1007/1-4020-4166-7_9

Cámara-Leret, R., Faurby, S., Macía, M. J., Balslev, H., Göldel, B., Svenning, J.-C., … Saslis-Lagoudakis, C. H. (2017). Fundamental species traits explain provisioning services of tropical American palms. *Nature Plants*, *3*(2). https://doi.org/10.1038/nplants.2016.220

Cassidy, A. (2018). Berry anthocyanin intake and cardiovascular health. *Molecular Aspects of Medicine*. https://doi.org/10.1016/j.mam.2017.05.002

Castillo-Lorenzo, E., Finch-Savage, W. E., Seal, C. E., & Pritchard, H. W. (2019). Adaptive significance of functional germination traits in crop wild relatives of Brassica. *Agricultural and Forest Meteorology*, *264*, 343–350.

Castillo-Lorenzo, E., Pritchard, H. W., Finch-Savage, W. E., & Seal, C. E. (2018). Comparison of seed and seedling functional traits in native Helianthus species and the crop H. annuus (sunflower). *Plant Biology*.

Cattivelli, L., Rizza, F., Badeck, F. W., Mazzucotelli, E., Mastrangelo, A. M., Francia, E., … Stanca, A. M. (2008). Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. *Field Crops Research*. https://doi.org/10.1016/j.fcr.2007.07.004

Challinor, A., Watson, J., Lobell, D., Howden, S., Smith, D., & Chhetri, N. (2014). A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, *4*, 287–291. https://doi.org/10.1038/nclimate2153

Chaudhary, P., & Initiatives, L. (2016). Consistency of local perceptions of climate change in the Kangchenjunga Himalaya Landscape Consistency of local perceptions of climate change in the Kangchenjunga Himalaya landscape. *Current Science*, *101*(4), 504–513.

Cheng, S., Melkonian, M., Smith, S. A., Brockington, S., Archibald, J. M., Delaux, P.-M., … Wong, G. K.-S. (2018). 10KP: A phylodiverse genome sequencing plan. *GigaScience*, *7*(3). https://doi.org/10.1093/gigascience/giy013

Chomicki, G., & Renner, S. S. (2014). Watermelon origin solved with molecular phylogenetics including Linnaean material: another example of museomics. *New Phytologist*, *205*(2), 526–532. https://doi.org/10.1111/nph.13163

Choudhary, K. K., & Agrawal, S. B. (2015). Assessment of Fatty Acid Profile and Seed Mineral Nutrients of Two Soybean (Glycine maxL.) Cultivars Under Elevated Ultraviolet-B: Role of ROS, Pigments and Antioxidants. *Photochemistry and Photobiology*, *92*(1), 134–143. https://doi.org/10.1111/php.12544

Christenhusz, M. J. M., Fay, M. F., & Chase, M. W. (2017). *Plants of the world : an illustrated encyclopedia of vascular plants*.

Cochrane, A., Yates, C. J., Hoyle, G. L., & Nicotra, A. B. (2015). Will among-population variation in seed

traits improve the chance of species persistence under climate change? *Global Ecology and Biogeography*, *24*(1), 12–24.

Colmer, T. D., Vos, H., & Pedersen, O. (2009). Tolerance of combined submergence and salinity in the halophytic stem-succulent Tecticornia pergranulata. *Annals of Botany*, *103*(2), 303–312. https://doi.org/10.1093/aob/mcn120

Coradin, L., Larranaga, N., van Zonneveld, M., Blonder, B., Hunter, D., & Hormaza, J. I. (2018). Human diets drive range expansion of megafauna-dispersed fruit species. *Proceedings of the National Academy of Sciences*, *115*(13), 3326–3331. https://doi.org/10.1073/pnas.1718045115

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, *28*(8), 482–488. https://doi.org/10.1016/j.tree.2013.04.003

Cristina Giannini, T., Acosta, A. L., Silva, C. I. da, de Oliveira, P. E. A. M., Imperatriz-Fonseca, V. L., & Saraiva, A. M. (2013). Identifying the areas to preserve passion fruit pollination service in Brazilian Tropical Savannas under climate change. *Agriculture, Ecosystems and Environment*, *171*(May), 39–46. https://doi.org/10.1016/j.agee.2013.03.003

Cronk, Q. C. (2008). Crop domestication in the Compositae : a family-wide trait assessment, 1141–1157. https://doi.org/10.1007/s10722-008-9315-0

Cronk, Q. C. B., & Forest, F. (2017). The Evolution of Angiosperm Trees: From Palaeobotany to Genomics. In *Comparative and Evolutionary Genomics of Angiosperm Trees* (pp. 1–17). https://doi.org/10.1007/7397

Crossa, J., Pérez-rodríguez, P., Cuevas, J., Montesinos-lópez, O., Jarquín, D., Campos, G. D. L., … Varshney, R. K. (2017). Genomic Selection in Plant Breeding : Methods , Models , and Perspectives. *Trends in Plant Science*, *xx*, 1–15. https://doi.org/10.1016/j.tplants.2017.08.011

Dai, X., Zhang, W., Xu, J., Duffy, K. J., & Guo, Q. (2017). Global pattern of plant utilization across different organisms: Does plant apparency or plant phylogeny matter? *Ecology and Evolution*, *7*(8), 2535–2545. https://doi.org/10.1002/ece3.2882

DaMatta, F. M., Grandis, A., Arenque, B. C., & Buckeridge, M. S. (2010). Impacts of climate changes on crop physiology and food quality. *Food Research International*, *43*(7), 1814–1823. https://doi.org/10.1016/j.foodres.2009.11.001

Delang, C. O. (2006). Not just minor forest products: The economic rationale for the consumption of wild food plants by subsistence farmers. *Ecological Economics*, 64–73. https://doi.org/10.1016/j.eco

Dempewolf, H., Eastwood, R. J., Guarino, L., Khoury, C. K., Müller, J. V., & Toll, J. (2014). Adapting Agriculture to Climate Change: A Global Initiative to Collect, Conserve, and Use Crop Wild Relatives. *Agroecology and Sustainable Food Systems*, *38*(4), 369–377. https://doi.org/10.1080/21683565.2013.870629

Deutsch, C. A., Tewksbury, J. J., & Tigchelaar, M. (2018). Increase in crop losses to insect pests in a warming climate, *919*(August), 916–919.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Donatelli, M., Srivastava, A. K., Duveiller, G., Niemeyer, S., & Fumagalli, D. (2015). Climate change impact and potential adaptation strategies under alternate realizations of climate scenarios for three major crops in Europe. *Environmental Research Letters*, *10*(7).

https://doi.org/10.1088/1748-9326/10/7/075005

Dong, J., Gruda, N., Lam, S. K., Li, X., & Duan, Z. (2018). Effects of Elevated CO2 on Nutritional Quality of Vegetables: A Review. *Frontiers in Plant Science*, *9*. https://doi.org/10.3389/fpls.2018.00924

Donohue, K. (2005). Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist*, *166*(1), 83–92. Retrieved from internal-pdf://0095503774/Donohue-2005-Niche construction through phenol.pdf

Dyer, L. A., Richards, L. A., Short, S. A., & Dodson, C. D. (2013). Effects of CO2 and Temperature on Tritrophic Interactions. *PLoS ONE*, *8*(4). https://doi.org/10.1371/journal.pone.0062528

Eckert, C. G., Kalisz, S., Geber, M. A., Sargent, R., Elle, E., Cheptou, P. O., … Winn, A. A. (2010). Plant mating systems in a changing world. *Trends in Ecology and Evolution*, *25*(1), 35–43. https://doi.org/10.1016/j.tree.2009.06.013

Edwards, E. J., Still, C. J., & Donoghue, M. J. (2007). The relevance of phylogeny to studies of global change, *22*(5). https://doi.org/10.1016/j.tree.2007.02.002

Egan, P. A., Adler, L. S., Irwin, R. E., Farrell, I. W., Palmer-young, E. C., Stevenson, P. C., … Egan, P. A. (2018). Crop Domestication Alters Floral Reward Chemistry With Potential Consequences for Pollinator Health, *9*(September), 1–14. https://doi.org/10.3389/fpls.2018.01357

Eiserhardt, W. L., Antonelli, A., Bennett, D. J., Botigué, L. R., Burleigh, J. G., Dodsworth, S., … Baker, W. J. (2018). A roadmap for global synthesis of the plant tree of life. *American Journal of Botany*, *105*(3), 614–622. https://doi.org/10.1002/ajb2.1041

Else, M. A., Janowiak, F., Atkinson, C. J., & Jackson, M. B. (2009). Root signals and stomatal closure in relation to photosynthesis, chlorophyll a fluorescence and adventitious rooting of flooded tomato plants. *Annals of Botany*, *103*(2), 313–323. https://doi.org/10.1093/aob/mcn208

Ernst, M., Saslis-Lagoudakis, C. H., Grace, O. M., Nilsson, N., Toft Simonsen, H., Horn, J. W., … Rønsted, N. (2016). Molecular phylogenetics as a predictive tool in plant-based drug discovery in the genus Euphorbia L. *Planta Medica*, *81*(S 01), S1–S381. https://doi.org/10.1055/s-0036-1596164

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity, 1–10.

Fanzo, J., Davis, C., McLaren, R., & Choufani, J. (2018). The effect of climate change across food systems: Implications for nutrition outcomes. *Global Food Security*, *18*, 12–19. https://doi.org/10.1016/j.gfs.2018.06.001

Farnsworth, N. R., & Soejarto, D. D. (1991). Global importance of medicinal plants. *The Conservation of Medicinal Plants*, *26*, 25–51.

Fernández-Pascual, E., Mattana, E., & Pritchard, H. W. (2018). Seeds of future past: climate change and the thermal memory of plant reproductive traits. *Biological Reviews*.

Fitter, A. H., & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants. *Science*, *296*(5573), 1689–1691. https://doi.org/10.1126/science.1071617

Food and Agriculture Organization of the United Nations. (2015). *FAO Statistical Pocketbook*. Food and Agriculture Organization of the United Nations.

Forbes, S.J., & Northfield, T. D. (2015). Increased pollinator habitat enhances cacao fruit set and predator conservation. *Ecological Applications*, *27*(3), 887–899. https://doi.org/10.1111/ijlh.12426

Forest, F., Grenyer, R., Rouget, M., Davies, T. J., Cowling, R. M., Faith, D. P., … Savolainen, V. (2007).

Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, *445*(February 2007), 757–760. https://doi.org/10.1038/nature05587

Fry, E. L., Evans, A. L., Sturrock, C. J., Bullock, J. M., & Bardgett, R. D. (2018). Root architecture governs plasticity in response to drought. *Plant and Soil*, *433*(1–2), 189–200. https://doi.org/10.1007/s11104-018-3824-1

Fu, Y. B. (2015). Understanding crop genetic diversity under modern plant breeding. *Theoretical and Applied Genetics*, *128*(11), 2131–2142. https://doi.org/10.1007/s00122-015-2585-y

Fuller, D. Q., Denham, T., Arroyo-kalin, M., Lucas, L., Stevens, C. J., Qin, L., & Allaby, R. G. (2014). Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record, *111*(17). https://doi.org/10.1073/pnas.1308937110

Garibaldi, L. A., Vanbergen, A. J., Biesmeijer, J. C., Aizen, M. A., Imperatriz-Fonseca, V., Ngo, H. T., … Potts, S. G. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

Garnatje, T., Peñuelas, J., & Vallès, J. (2017). Ethnobotany, Phylogeny and "Omics" for Human Health and Food Security. *Trends in Plant Science*, *22*(3), 187–191. https://doi.org/10.1016/j.tplants.2017.01.001

Garnett, S. T., Fernández-Llamazares, Á., Brondizio, E. S., Duncan, T., Malmer, P., Jonas, H., … Geyle, H. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability*, *1*(7), 369–374. https://doi.org/10.1038/s41893-018-0100-6

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., … Toulmin, C. (2010). Food Security : The Challenge of Feeding 9 Billion People. *Science*, *327*(February), 812–818. https://doi.org/DOI: 10.1126/science.1185383

Gordo, O., & Sanz, J. J. (2005). Phenology and climate change: A long-term study in a Mediterranean locality. *Oecologia*, *146*(3), 484–495. https://doi.org/10.1007/s00442-005-0240-z

Gray, S. B., & Brady, S. M. (2016). Plant developmental responses to climate change. *Developmental Biology*, *419*(1), 64–77. https://doi.org/10.1016/j.ydbio.2016.07.023

Green, H., Broun, P., Cook, D., Cooper, K., Drewnowski, A., Pollard, D., … Roulin, A. (2018). Healthy and sustainable diets for future generations. *Journal of the Science of Food and Agriculture*, *98*(9), 3219–3224. https://doi.org/10.1002/jsfa.8953

Groeneveld, J. H., Tscharntke, T., Moser, G., & Clough, Y. (2010). Experimental evidence for stronger cacao yield limitation by pollination than by plant resources. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*(3), 183–191. https://doi.org/10.1016/j.ppees.2010.02.005

Gross, B. L., & Zhao, Z. (2014). Archaeological and genetic insights into the origins of domesticated rice. *Proceedings of the National Academy of Sciences*, *111*(17), 6190–6197. https://doi.org/10.1073/pnas.1308942110

Guo, Z., Zhang, L., & Li, Y. (2010). Increased dependence of humans on ecosystem services and biodiversity. *PLoS ONE*, *5*(10). https://doi.org/10.1371/journal.pone.0013113

Gurr, G. M., Wratten, S. D., Landis, D. A., & You, M. (2016). Habitat Management to Suppress Pest Populations: Progress and Prospects. *Annual Review of Entomology*, *62*(1), 91–109. https://doi.org/10.1146/annurev-ento-031616-035050

Halse-Gramkow, M., Ernst, M., Dunn, R. R., & Saslis-Lagoudakis, C. H. (2016). Phylogenetics of psychoactive plants in neuro-targeted bioprospecting. *Planta Medica*, *81*(S 01), S1–S381. https://doi.org/10.1055/s-0036-1596186

Hammer, K., & Khoshbakht, K. (2015). A domestication assessment of the big five plant families. *Genetic Resources and Crop Evolution*, *62*(5), 665–689. https://doi.org/10.1007/s10722-014-0186-2

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*(5), 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Harlan, J. (1971). Agricultural Origins: Centers and Noncenters. *Science*, *239*(4843), 17–18.

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Hill, J. (2007). Review article Environmental costs and benefits of transportation biofuel production from food- and lignocellulose-based energy crops . A review. *Agronomy for Sustainable Development*, *27*, 1–12. https://doi.org/10.1051/agro

Hoffmann, A. A., & Sgró, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Holopainen, J. K., Blande, J. D., Virjamo, V., Ghimire, R. P., Julkunen-Tiitto, R., & Kivimäenpää, M. (2018). Climate Change Effects on Secondary Compounds of Forest Trees in the Northern Hemisphere. *Frontiers in Plant Science*, *9*(October), 1–10. https://doi.org/10.3389/fpls.2018.01445

Howes, M. J. R., & Simmonds, M. S. J. (2014). The role of phytochemicals as micronutrients in health and disease. *Current Opinion in Clinical Nutrition and Metabolic Care*, *17*(6), 558–566. https://doi.org/10.1097/MCO.0000000000000115

Hummel, M., Hallahan, B. F., Brychkova, G., Ramirez-Villegas, J., Guwela, V., Chataika, B., … Spillane, C. (2018). Reduction in nutritional quality and growing area suitability of common bean under climate change induced drought stress in Africa. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-33952-4

IPCC. (2013). IPCC Fifth Assessment Report (AR5) - The physical science basis. *IPCC*.

Jin, J., Armstrong, R., & Tang, C. (2019). Impact of elevated CO2 on grain nutrient concentration varies with crops and soils – A long-term FACE study. *Science of The Total Environment*, *651*, 2641–2647. https://doi.org/10.1016/j.scitotenv.2018.10.170

Kadam, N. N., Xiao, G., Melgar, R. J., Bahuguna, R. N., Quinones, C., Tamilselvan, A., … Jagadish, K. S. V. (2014). Chapter Three - Agronomic and Physiological Responses to High Temperature, Drought, and Elevated CO2 Interactions in Cereals. In D. B. T.-A. in A. Sparks (Ed.) (Vol. 127, pp. 111–156). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-800131-8.00003-0

Kelly, S., Grenyer, R., & Scotland, R. W. (2014). Phylogenetic trees do not reliably predict feature diversity. *Diversity and Distributions*, *20*, 600–612. https://doi.org/10.1111/ddi.12188

Kering, M. K., Guretzky, J., Funderburg, E., & Mosali, J. (2011). Effect of Nitrogen Fertilizer Rate and Harvest Season on Forage Yield, Quality, and Macronutrient Concentrations in Midland Bermuda Grass. *Communications in Soil Science and Plant Analysis*, *42*, 1958–1971. https://doi.org/10.1080/00103624.2011.591470

Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., … Gall, L. F. (2015). Climate change impacts on bumblebees converge across continents. *Science*, *349*(6244), 177–180.

Khoury, C. K., Achicanoy, H. A., Bjorkman, A. D., Navarro-Racines, C., Guarino, L., Flores-Palacios, X., …

Struik, P. C. (2016). Origins of food crops connect countries worldwide. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1832), 1–9. https://doi.org/10.1098/rspb.2016.0792

Khoury, C. K., Ramirez-Villegas, J., Guarino, L., Bjorkman, A. D., Dempewolf, H., Rieseberg, L. H., … Struik, P. C. (2014). Increasing homogeneity in global food supplies and the implications for food security. *Proceedings of the National Academy of Sciences*, *111*(11), 4001–4006. https://doi.org/10.1073/pnas.1313490111

Kochanek, J., Buckley, Y. M., Probert, R. J., Adkins, S. W., & Steadman, K. J. (2010). Pre-zygotic parental environment modulates seed longevity. *Austral Ecology*, *35*(7), 837–848. Retrieved from internal-pdf://83.244.69.127/Kochanek-2010-Pre-zygotic parental environment.pdf

Kulkarni, K. P., Tayade, R., Asekova, S., Song, J. T., Shannon, J. G., & Lee, J.-D. (2018). Harnessing the Potential of Forage Legumes, Alfalfa, Soybean, and Cowpea for Sustainable Agriculture and Global Food Security. *Frontiers in Plant Science*, *9*. https://doi.org/10.3389/fpls.2018.01314

Laenoi, S., Rerkasem, B., Lordkaew, S., & Prom-u-thai, C. (2018). Seasonal variation in grain yield and quality in different rice varieties. *Field Crops Research*, *221*, 350–357. https://doi.org/10.1016/j.fcr.2017.06.006

Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary Ecology*, *30*(2), 191–202.

Larkindale, J., & Huang, B. (2004). Thermotolerance and antioxidant systems in Agrostis stolonifera: Involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide, and ethylene. *Journal of Plant Physiology*, *161*(4), 405–413. https://doi.org/10.1078/0176-1617-01239

Lee, M. A., Davis, A. P., Chagunda, M. G. G., & Manning, P. (2017). Forage quality declines with rising temperatures, with implications for livestock production and methane emissions. *Biogeosciences*, *14*(6), 1403–1417. https://doi.org/10.5194/bg-14-1403-2017

Lee, M., Manning, P., Rist, J., Power, S. A., & Marsh, C. (2010). A global comparison of grassland biomass responses to CO2 and nitrogen enrichment. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1549), 2047–2056. https://doi.org/10.1098/rstb.2010.0028

Li, D., & Pritchard, H. W. (2009). The science and economics of ex situ plant conservation, (October). https://doi.org/10.1016/j.tplants.2009.09.005

Lobell, D. B., & Field, C. B. (2007). Global scale climate-crop yield relationships and the impacts of recent warming. *Environmental Research Letters*, *2*(1). https://doi.org/10.1088/1748-9326/2/1/014002

Lobell, D., Schlenker, W., & Costa-Roberts, J. (2011). Climate Trends and Global crop production since 1980. *Science*, *333*(June), 1186–1189.

Loladze, I. (2014). Hidden shift of the ionome of plants exposed to elevated CO2 depletes minerals at the base of human nutrition. *ELife*, *2014*(3), 1–29. https://doi.org/10.7554/eLife.02245

Long, R. L., Gorecki, M. J., Renton, M., Scott, J. K., Colville, L., Goggin, D. E., … Finch-Savage, W. E. (2015). The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. *Biological Reviews*, *90*(1), 31–59. Retrieved from internal-pdf://80.19.69.64/Long-2015-The ecophysiology of seed persistenc.pdf

Makondo, C., & Thomas, D. S. G. (2018). Climate change adaptation : Linking indigenous knowledge with western science for e ff ective adaptation. *Environmental Science and Policy*, *88*(January), 83–91. https://doi.org/10.1016/j.envsci.2018.06.014

Matzke, N. J. (2018). BioGeoBEARS: BioGeography with Bayesian (and likelihood) Evolutionary Analysis with R Scripts (Version v1.1.1).

McClure, K. A., Sawler, J., Gardner, K. M., Money, D., & Myles, S. (2014). Genomics: A potential panacea for the perennial problem. *American Journal of Botany*, *101*(10), 1780–1790. https://doi.org/10.3732/ajb.1400143

Mehrabi, Z., Pironon, S., Kantar, M., Ramankutty, N., & Rieseberg, L. (2019). Shifts in the abiotic and biotic environment of cultivated sunflower under future climate change.

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, *10*(8), 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Meyer, R. S., Duval, A. E., & Jensen, H. R. (2012). Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist*, *196*, 29–48.

Meyer, R. S., & Purugganan, M. D. (2013). Evolution of crop species: genetics of domestication and diversification. *Nature Reviews Genetics*, *14*, 840. Retrieved from https://doi.org/10.1038/nrg3605

Miller, A. J., & Gross, B. L. (2011). From forest to field: Perennial fruit crop domestication. *American Journal of Botany*, *98*(9), 1389–1414. https://doi.org/10.3732/ajb.1000522

Moat, J., Williams, J., Baena, S., Wilkinson, T., Gole, T. W., Challa, Z. K., … Davis, A. P. (2017). Resilience potential of the Ethiopian coffee sector under climate change. *Nature Plants*, *3*(7), 17081. https://doi.org/10.1038/nplants.2017.81

Moerman, D. E. (1991). The medicinal flora of native North America: An analysis. *Journal of Ethnopharmacology*, *31*, 1–42.

Mollel, N. P., Fischer, M., Hemp, A., & Fischer, M. (2017). Usable wild plant species in relation to elevation and land use at Mount Kilimanjaro , Tanzania. *Alpine Botany*, *127*(2), 145–154. https://doi.org/10.1007/s00035-017-0187-9

Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., … Yahara, T. (2009). Biodiversity, climate change, and ecosystem services. *Current Opinion in Environmental Sustainability*, *1*(1), 46–54. https://doi.org/10.1016/j.cosust.2009.07.006

Morueta-Holme, N., Jonas, J. D., Segnitz, R. M., Svenning, J.-C., Sandoval-Acuña, P., & Engemann, K. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences*, *112*(41), 12741–12745. https://doi.org/10.1073/pnas.1509938112

Muller, C., Cramer, W., Hare, W. L., & Lotze-Campen, H. (2011). Climate change risks for African agriculture. *Proceedings of the National Academy of Sciences*, *108*(11), 4313–4315. https://doi.org/10.1073/pnas.1015078108

Muthayya, S., Sugimoto, J. D., Montgomery, S., & Maberly, G. F. (2014). An overview of global rice production, supply, trade, and consumption. *Annals of the New York Academy of Sciences*, *1324*(1), 7–14. https://doi.org/10.1111/nyas.12540

Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Lysenko, I., Palma, A. De, … Purvis, A. (2016). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide, 1–24. https://doi.org/10.5519/0066354

Odgaard, M. V., Bøcher, P. K., Dalgaard, T., & Svenning, J. C. (2011). Climatic and non-climatic drivers

of spatiotemporal maize-area dynamics across the northern limit for maize production-A case study from Denmark. *Agriculture, Ecosystems and Environment*, *142*(3–4), 291–302. https://doi.org/10.1016/j.agee.2011.05.026

Ogle, B. M., Tuyet, H. T., Duyet, H. N., Dung, N. N. X., & Xuan Dung, N. N. (2003). Food, Feed or Medicine: The Multiple Functions of Edible Wild Plants in Vietnam. *Economic Botany*, *57*(1), 103–117. https://doi.org/10.1663/0013-0001(2003)057[0103:FFOMTM]2.0.CO;2

Oguchi, R., Ozaki, H., Hanada, K., & Hikosaka, K. (2016). Which plant trait explains the variations in relative growth rate and its response to elevated carbon dioxide concentration among Arabidopsis thaliana ecotypes derived from a variety of habitats? *Oecologia*, *180*(3), 865–876. https://doi.org/10.1007/s00442-015-3479-z

Ohlemüller, R., Anderson, B. J., Araújo, M. B., Butchart, S. H. M., Kudrna, O., Ridgely, R. S., & Thomas, C. D. (2008). The coincidence of climatic and species rarity: High risk to small-range species from climate change. *Biology Letters*, *4*(5), 568–572. https://doi.org/10.1098/rsbl.2008.0097

Ooi, M. K. J., Denham, A. J., Santana, V. M., & Auld, T. D. (2014). Temperature thresholds of physically dormant seeds and plant functional response to fire: variation among species and relative impact of climate change. *Ecology and Evolution*, *4*(5), 656–671. Retrieved from internal-pdf://0355681663/Ooi-2014-Temperature thresholds of physically.pdf

Ortiz, R., Jarvis, A., Fox, P., Aggarwal, P. K., & Campbell, B. M. (2014). *Plant genetic engineering, climate change and food security*.

Otto, S. P. (2018). Adaptation, speciation and extinction in the Anthropocene. *Proc. R. Soc. B*, *285*(1891), 20182047. https://doi.org/10.1098/RSPB.2018.2047

Owen, N. R., Gumbs, R., Gray, C. L., & Faith, D. P. (2019). captures more than just functional diversity. *Nature Communications*, 8–10. https://doi.org/10.1038/s41467-019-08600-8

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*, 215. Retrieved from https://doi.org/10.1038/nclimate2448

Padulosi, S., Heywood, V., Hunter, D., & Jarvis, A. (2011). Underutilized species and climate change: current status and outlook. *Crop Adaptation to Climate Change*, 507–521. https://doi.org/10.1002/9780470960929

Parejko, K. (2003). Pliny the Elder's Silphium: First Recorded Species Extinction. *Conservation Biology*, *17*(3), 925–927. https://doi.org/10.1007/s10669-006-7484-y

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/science.aai9214

Peña-Fronteras, J. T., Villalobos, M. C., Baltazar, A. M., Merca, F. E., Ismail, A. M., & Johnson, D. E. (2009). Adaptation to flooding in upland and lowland ecotypes of Cyperus rotundus, a troublesome sedge weed of rice: Tuber morphology and carbohydrate metabolism. *Annals of Botany*, *103*(2), 295–302. https://doi.org/10.1093/aob/mcn085

Penuelas, J. (2002). Responses to a Warming World. *Science*, *294*(5543), 793–795. https://doi.org/10.1126/science.1066860

Pingali, P. L. (2012). Green Revolution: Impacts, limits, and the path ahead. *Proceedings of the National Academy of Sciences*, *109*(31), 12302–12308. https://doi.org/10.1073/pnas.0912953109

Pironon, S., Etherington, T. R., Borrell, J. S., Kuhn, N., Macias-Fauria, M., Ondo, I., … Willis, K. J. (n.d.).

Potential adaptive strategies for 29 Sub-Saharan crops under future climate change (*accepted*, Nature Climate Change).

Pironon, S., Ondo, I., Diazgranados, M., Baquero, A. C., Allkin, R., Canteiro, C., … Willis, K. J. (n.d.). Exploring the global distribution of people's plants. (Under review).

Polce, C., Garratt, M. P., Termansen, M., Ramirez-Villegas, J., Challinor, A. J., Lappage, M. G., … Biesmeijer, J. C. (2014). Climate-driven spatial mismatches between British orchards and their pollinators: Increased risks of pollination deficits. *Global Change Biology*, *20*(9), 2815–2828. https://doi.org/10.1111/gcb.12577

Porceddu, M., Mattana, E., Pritchard, H. W., & Bacchetta, G. (2017). Dissecting seed dormancy and germination in Aquilegia barbaricina, through thermal kinetics of embryo growth. *Plant Biology*, *19*(6), 983–993. Retrieved from internal-pdf://62.46.69.111/Porceddu-2017-Dissecting seed dormancy and ger.pdf

Pritchard, H. W. (2016). Priority science for the preservation of priority crops. *Indian J Plant Genet Resour*, *29*, 297.

Pritchard, H. W. (2018). The rise of plant cryobiotechnology and demise of plant cryopreservation? *Cryobiology*, *85*, 160–161.

Qian, H., & Ricklefs, R. E. (2016). Out of the Tropical Lowlands: Latitude versus Elevation. *Trends in Ecology and Evolution*, *31*(10), 738–741. https://doi.org/10.1016/j.tree.2016.07.012

RBG Kew. (2016). State of the World's Plants 2016. *Royal Botanic Gardens, Kew*, 1–80. https://doi.org/10.1287/mnsc.1070.0706

Richardson, J. E., Whitlock, B. A., Meerow, A. W., & Madriñán, S. (2015). The age of chocolate: a diversification history of Theobroma and Malvaceae. *Frontiers in Ecology and Evolution*, *3*(November), 1–14. https://doi.org/10.3389/fevo.2015.00120

Robbirt, K. M., Roberts, D. L., Hutchings, M. J., & Davy, A. J. (2014). Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Current Biology*, *24*(23), 2845–2849. https://doi.org/10.1016/j.cub.2014.10.033

Rodríguez, M. A., Angueyra, A., Cleef, A. M., & Van Andel, T. (2018). Ethnobotany of the Sierra Nevada del Cocuy-Güicán: Climate change and conservation strategies in the Colombian Andes. *Journal of Ethnobiology and Ethnomedicine*, *14*(1), 1–12. https://doi.org/10.1186/s13002-018-0227-6

Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., … Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, *356*(6339), 742 LP-744. https://doi.org/10.1126/science.aaj1631

Rudman, S. M., Kreitzman, M., Chan, K. M. A., & Schluter, D. (2017). Evosystem Services : Rapid Evolution and the Provision of Ecosystem Services. *Trends in Ecology & Evolution*, *32*(6), 403–415. https://doi.org/10.1016/j.tree.2017.02.019

Rumpf, S. B., Willner, W., Schütz, M., Dullinger, S., Moser, D., Wessely, J., … Klonner, G. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences*, *115*(8), 1848–1853. https://doi.org/10.1073/pnas.1713936115

Ryan, P. (2018). *Nubia Past and Present; agriculture, crops and food*. London and Khartoum: The British Museum.

Saslis-Lagoudakis, C. H., Savolainen, V., Williamson, E. M., Forest, F., Wagstaff, S. J., Baral, S. R., … Hawkins, J. A. (2012). Phylogenies reveal predictive power of traditional medicine in bioprospecting. *Proceedings of the National Academy of Sciences*, *109*(39), 15835–15840.

https://doi.org/10.1073/pnas.1202242109

Saupe, E. E., Portell, R. W., Qiao, H., Soberón, J., Hendricks, J. R., Lieberman, B. S., & Hunter, S. J. (2015). Niche breadth and geographic range size as determinants of species survival on geological time scales. *Global Ecology and Biogeography*, *24*(10), 1159–1169. https://doi.org/10.1111/geb.12333

Schippmann, U., Leaman, D. J., & Cunningham, A. B. (2002). *Impact of Cultivation and Gathering of Medicinal Plants on Biodiversity: Global Trends and Issues*. *Materials Science Research International* (Vol. 3). https://doi.org/10.1515/hfsg.1998.52.4.365

Schlenker, W., & Lobell, D. B. (2010). Robust negative impacts of climate change on African agriculture. *Environmental Research Letters*, *5*(1). https://doi.org/10.1088/1748-9326/5/1/014010

Schroth, G., Läderach, P., Blackburn Cuero, D. S., Neilson, J., & Bunn, C. (2015). Winner or loser of climate change? A modeling study of current and future climatic suitability of Arabica coffee in Indonesia. *Regional Environmental Change*, *15*(7), 1473–1482. https://doi.org/10.1007/s10113-014-0713-x

Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees, 1041–1049. https://doi.org/10.1007/s00442-014-2960-4

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate Change Can Cause Spatial Mismatch of Trophically Interacting Species. *Ecology*, *89*(12), 3472–3479.

Şerban, P., Wilson, J. R. U., Vamosi, J. C., & Richardson, D. M. (2008). Plant Diversity in the Human Diet: Weak Phylogenetic Signal Indicates Breadth. *BioScience*, *58*(2), 151–159. https://doi.org/10.1641/b580209

Settele, J., Bishop, J., & Potts, S. G. (2016). Climate change impacts on pollination. *Nature Plants*, *2*(7). https://doi.org/10.1038/nplants.2016.92

Shah, F., Huang, J., Cui, K., Nie, L., Shah, T., Chen, C., & Wang, K. (2011). Impact of high-temperature stress on rice plant and its traits related to tolerance. *Journal of Agricultural Science*, *149*(5), 545–556. https://doi.org/10.1017/S0021859611000360

Smith, B. D. (2007). Niche construction and the behavioral context of plant and animal domestication. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *16*(5), 188–199. Retrieved from internal-pdf://240.30.69.80/Smith-2007-Niche construction and the behavior.pdf

Smýkal, P., Coyne, C. J., Ambrose, M. J., Maxted, N., Schaefer, H., Blair, M. W., … Varshney, R. K. (2014). Legume Crops Phylogeny and Genetic Diversity for Science and Breeding. *Critical Reviews in Plant Sciences*, *34*(1–3), 43–104. https://doi.org/10.1080/07352689.2014.897904

Smýkal, P., Nelson, M., Berger, J., & von Wettberg, E. (2018). The Impact of Genetic Changes during Crop Domestication on Healthy Food Development. *Agronomy*, *8*(3), 26. https://doi.org/10.3390/agronomy8030026

Solga, M. J., Harmon, J. P., & Ganguli, A. C. (2014). Timing is Everything: An Overview of Phenological Changes to Plants and Their Pollinators. *Natural Areas Journal*, *34*(2), 227–234. https://doi.org/10.3375/043.034.0213

Soltis, P. S., & Soltis, D. E. (2016). Ancient WGD events as drivers of key innovations in angiosperms. *Current Opinion in Plant Biology*, *30*, 159–165. https://doi.org/10.1016/j.pbi.2016.03.015

Springate, D. A., & Kover, P. X. (2014). Plant responses to elevated temperatures: A field study on

phenological sensitivity and fitness responses to simulated climate warming. *Global Change Biology*, *20*(2), 456–465. https://doi.org/10.1111/gcb.12430

Svenning, A. J., Normand, S., Skov, F., Svenning, J., Normand, S., & Skov, F. (2008). Postglacial Dispersal Limitation of Widespread Forest Plant Species in Nemoral Europe. *Ecographyphy*, *31*(3), 316–326. https://doi.org/10.1111/j.2008.0906-7590.05206.x

Teixeira, E. I., Fischer, G., Velthuizen, H. Van, Walter, C., & Ewert, F. (2013). Global hot-spots of heat stress on agricultural crops due to climate change. *Agricultural and Forest Meteorology*, *170*, 206–215. https://doi.org/10.1016/j.agrformet.2011.09.002

Thorne, J. H., Fordyce, J. A., Forister, M. L., Shapiro, A. M., McCall, A. C., O'Brien, J., … Waetjen, D. P. (2010). Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences*, *107*(5), 2088–2092. https://doi.org/10.1073/pnas.0909686107

Ulian, T., Pritchard, H. W., Cockel, C. P., & Mattana, E. (2019). *Enhancing food security through seed banking and use of wild plants: case studies from the Royal Botanic Gardens, Kew. In Encyclopedia of Food Security and Sustainability*. (P. Ferranti, E. Berry, & A. Jock, Eds.). New York: Elsevier.

Vamosi, J. C., & Wilson, J. R. U. (2008). Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecology Letters*, *11*, 1047–1053. https://doi.org/10.1111/j.1461-0248.2008.01215.x

Vanbergen, A. J., Garratt, M. P., Vanbergen, A. J., Baude, M., Biesmeijer, J. C., Britton, N. F., … Wright, G. A. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251–259. https://doi.org/10.1890/120126

VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., & Reside, A. E. (2012). Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, *3*, 239. Retrieved from https://doi.org/10.1038/nclimate1688

Vaughan, D. A., Balázs, E., & Heslop-Harrison, J. S. (2007). From crop domestication to super-domestication. *Annals of Botany*, *100*(5), 893–901. https://doi.org/10.1093/aob/mcm224

Vuuren, D. P. van, Sala, O. E., & Pereira, H. M. (2006). The Future of Vascular Plant Diversity Under Four Global Scenarios. *Ecology and Society*, *11*(2).

Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. R. (2007). Heat tolerance in plants: An overview. *Environmental and Experimental Botany*. https://doi.org/10.1016/j.envexpbot.2007.05.011

Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, *17*(6), 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

Walters, C., Wheeler, L., & Stanwood, P. C. (2004). Longevity of cryogenically stored seeds. *Cryobiology*, *48*(3), 229–244. Retrieved from internal-pdf://83.125.69.111/Walters-2004-Longevity of cryogenically stored.pdf

Warren, J., Misir, S., & Kalai. (1995). Isozyme markers for self-compatibility and yield in theobroma cacao (Cacao). *Heredity*, *74*(4), 354–356. https://doi.org/10.1038/hdy.1995.53

Warren, T. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*(169), 65–69. https://doi.org/10.1093/nq/s7-VII.169.229-b

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and

disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, *104*(14), 5738–5742. https://doi.org/10.1073/pnas.0606292104

Wyse, S. V, & Dickie, J. B. (2017). Predicting the global incidence of seed desiccation sensitivity. *Journal of Ecology*, *105*(4), 1082–1093.

Yemataw, Z., Tesfaye, K., Zeberga, A., & Blomme, G. (2016). Exploiting indigenous knowledge of subsistence farmers' for the management and conservation of Enset (Ensete ventricosum (Welw.) Cheesman) (musaceae family) diversity on-farm. *Journal of Ethnobiology and Ethnomedicine*, *12*(1), 34. https://doi.org/10.1186/s13002-016-0109-8

Yu, G., Smith, D. K., Zhu, H., Guan, Y., & Lam, T. T. (2017). GGTREE : an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data, 28–36. https://doi.org/10.1111/2041-210X.12628

Zeven, A., & de Wet, J. (1982). *Dictionary of cultivated plants and their regions of diversity*. https://doi.org/10.1016/j.contraception.2015.02.004

Ziska, L. H., Epstein, P. R., & Schlesinger, W. H. (2009). Commentary Rising CO 2 , Climate Change , and Public Health : Exploring the Links to Plant Biology, *117*(2), 155–158. https://doi.org/10.1289/ehp.11501

## Figure Legends

**Figure 1. A schematic diagram of the potential distribution of useful plants across the domestication spectrum.** The total number of useful plants is reported as exceeding 31,000 (Kew, 2016), however the actual and relative size of domestication classes is unknown.

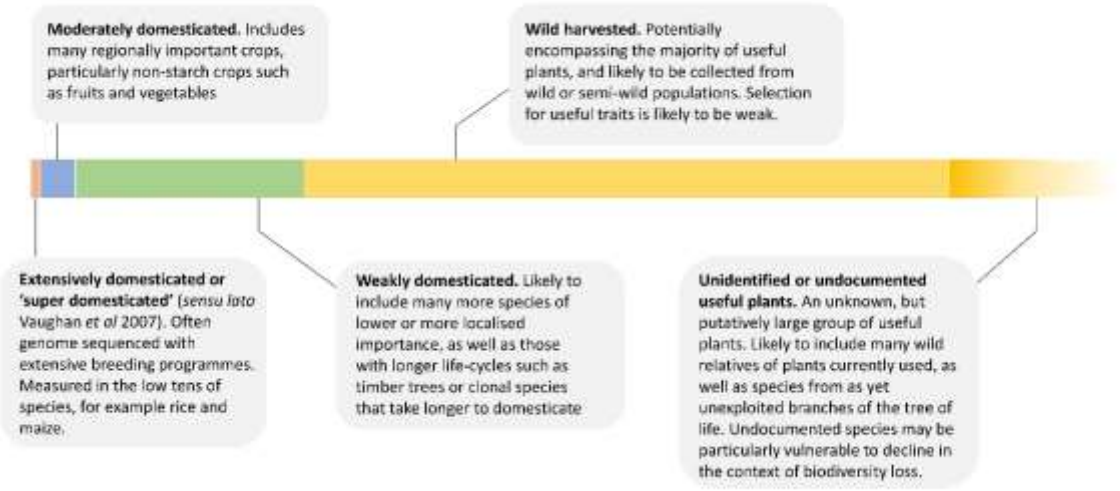


**Figure 2. climate change adaptation strategies and trade-offs for the future utilization of useful plants.**

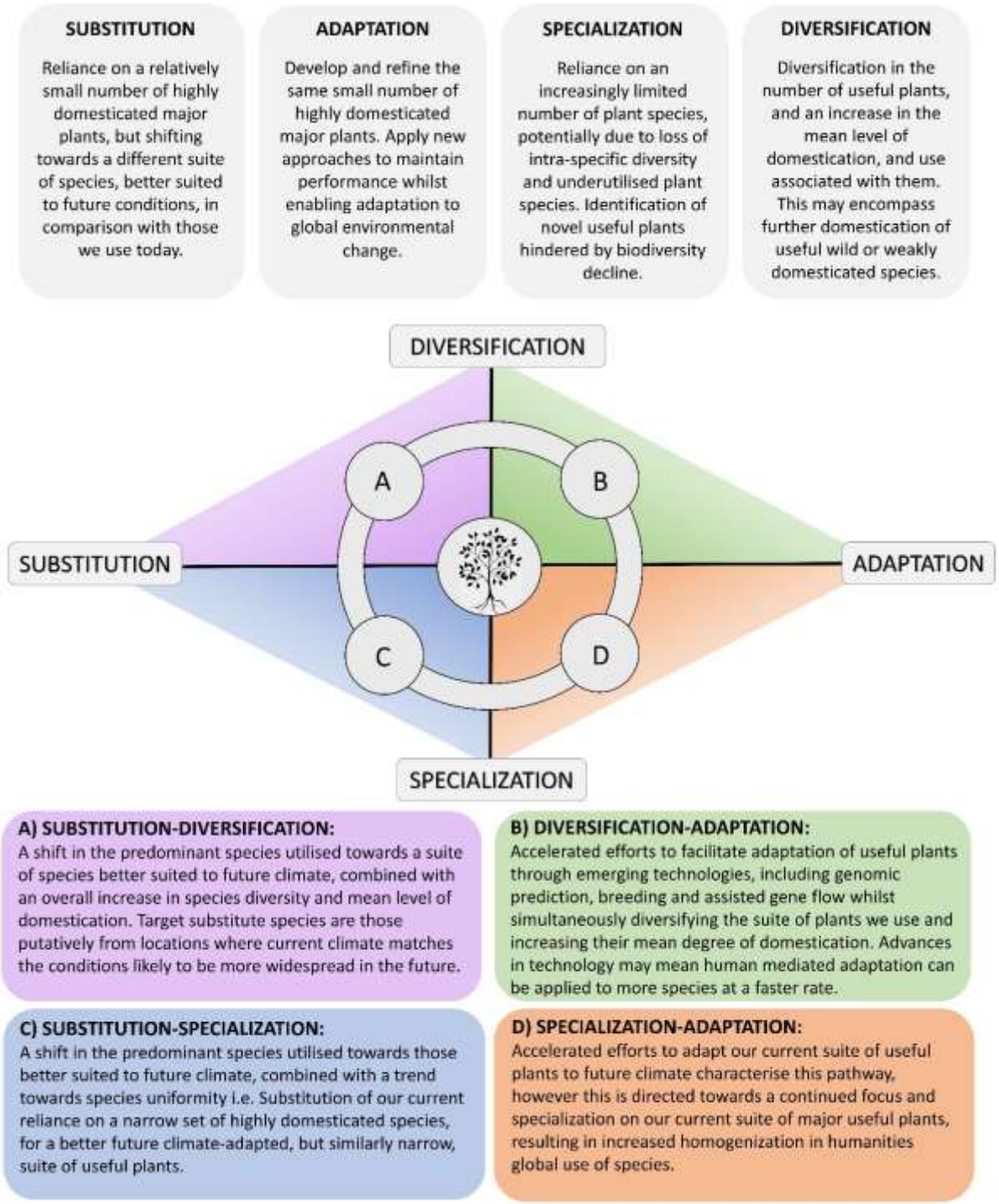


**Figure 3. Phylogenetic distribution of selected plant crops across the seed plant families.** A) Crops species were identified *sensu* FAO (2010). Families containing at least one crop taxon are indicated with red bars placed in front of the phylogenetic tips. Plant families without any crop are colour coded in blue. We note however that families without crop taxa may nevertheless include useful plants not considered in this analysis. A bar plot with the proportion (%) of crop plant taxa per number of species

is also provided. A familial phylogeny of seed plants was produced by collapsing species into families using the R package BioGeoBEARS (Matzke, 2018) while crop plant families were plotted as trait data in phylogenetic tips using the R package ggtree (Yu, Smith, Zhu, Guan, & Lam, 2017). The total number of species per family was obtained from Christenhusz et al. (2017).

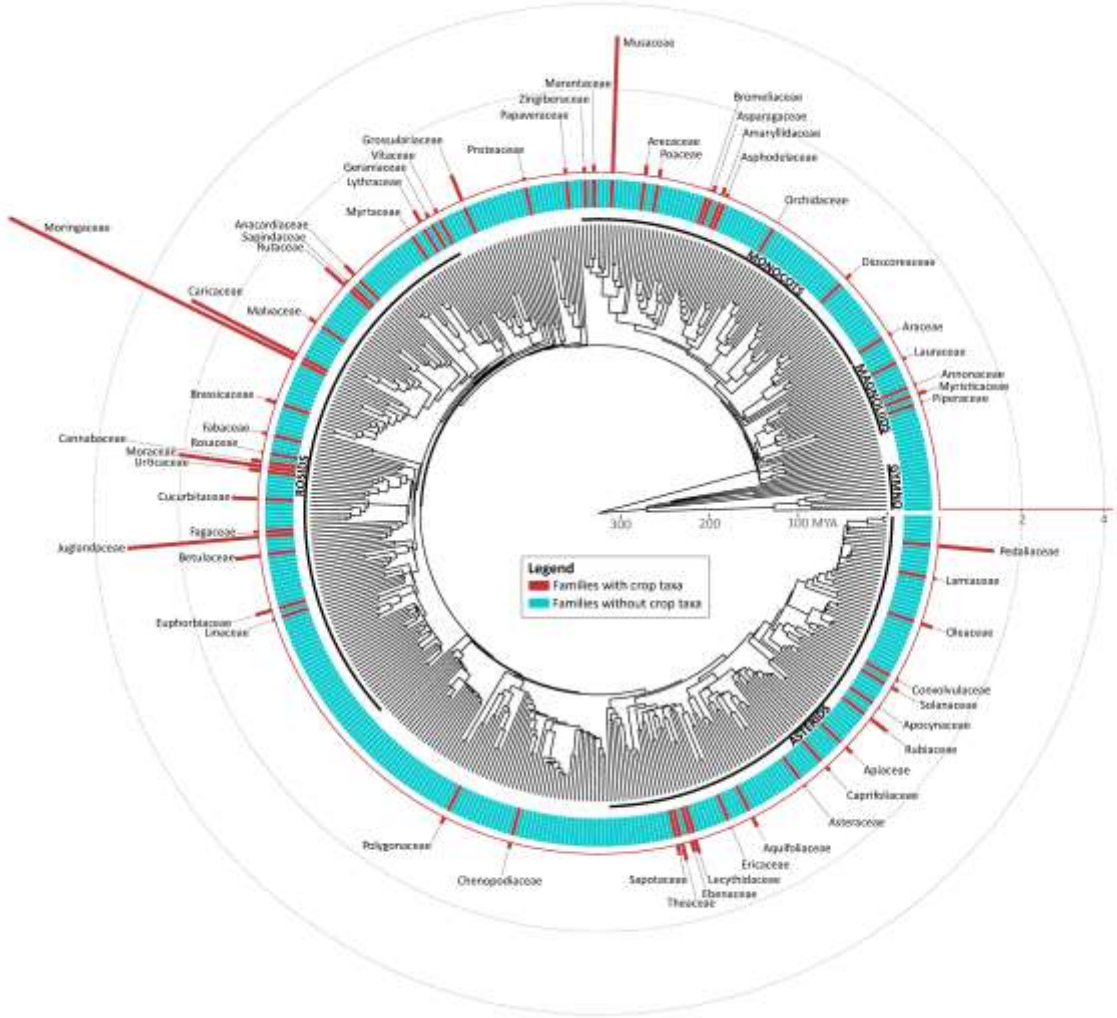


**Figure 4. Traits that are likely to characterise future useful plants under climate change.** Schematic diagram with a non-exhaustive selection of desirable useful plant traits in response to a range of emerging environmental stressors associated with climate change.